

# TAXONOMY OF *THERMOPSIS* (FABACEAE) IN NORTH AMERICA<sup>1</sup>

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## ABSTRACT

Comprehensive reevaluation of both herbarium specimens and field observations of the North American *Thermopsis* leads to our recognition of 10 species. Three species occur in the southern Appalachians: *T. villosa*, *T. mollis*, and *T. fraxinifolia*. The Rocky Mountains and intermountain regions are populated by the relatively variable and widespread species *T. divaricarpa*, *T. montana*, and *T. rhombifolia*. The Pacific coastal mountains of California are dominated by the variable *T. californica* (with three infraspecific taxa), which gives way to *T. gracilis* in northern California and western Oregon. *Thermopsis macrophylla* and *T. robusta* have restricted ranges in California.

Widely distributed throughout the western and southeastern United States, *Thermopsis* is a conspicuous, often weedy genus. Though it is a herbaceous plant, its relatively large habit and stunning racemes of golden or bright yellow flowers and flattened, rattling pods have no doubt contributed to its early and thorough collection. These factors, perhaps, should have led to a clear understanding of its systematics, but a lack of diagnostic characters within the genus, morphological intergradation, and possible hybridization have complicated the taxonomy of *Thermopsis*. Modern treatments (e.g., Isely, 1981) include from 4 to 10 species in North America, though over 20 specific names have been proposed.

The current study is based on over 20,000 km of roadside field study in North America (spanning 25 years for B. Turner), greenhouse studies (by M. Mendenhall), and the examination of approximately 6000 herbarium specimens (by all of the authors). We find 10 species of *Thermopsis* in North America. This treatment differs from earlier evaluations primarily in the rank and affiliations of taxa in the western United States. While an extreme perspective would combine the western taxa into two highly variable species, we recognize four species in the Pacific coastal states, three of which have restricted ranges, and three widely distributed

species in the Rocky Mountain and intermountain regions. The three long-recognized species of the southeastern United States are maintained.

The following herbaria have generously supplied the approximately 6000 specimens used in this study (number of sheets loaned given in parentheses): ARIZ (113), CAS (516), COLO (181), F (193), GH (511), JEPS (16), LL (15), MO (444), MONTU (91), NCU (112), ND (99), NEBC (3), NY (715), ORE (78), OSC (85), PE (52), PH (193), POM (75), RM (611), RSA (302), TENN (71), TEX (163), UC (401), US (419), UT (83), WS (161), WTU (200).

## HISTORY OF THE GENUS

*Thermopsis* (Greek "thermos" = lupine + "opsis" = appearance) was originally included in *Sophora* by Linnaeus (1753). Willdenow (1799) placed the taxon in *Podalyria*. In 1811, Robert Brown erected *Thermopsis* based upon *Sophora lupinoides* L. Brown renamed the latter *Thermopsis lanceolata*, which is contrary to the present Code of Botanical Nomenclature (Greuter et al., 1988); the name *Thermopsis lupinoides* (L.) Link, erected in 1821 and recognized still, precludes the use of this specific epithet for the type species of the genus. In 1818, Nuttall called the genus *Ther-*

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*mia*. Rafinesque erected the genera *Scolobus* and *Drepilia* in 1819, both based on specimens of *Thermopsis rhombifolia*.

Larisey (1940) revised the North American *Thermopsis* because she saw considerable "taxonomic confusion," which she eventually ascribed to "bibliographical" problems. She distilled 22 published names to 10 species by reducing the 4 southeastern species to 3 and 18 western species to 7. St. John (1941) responded to Larisey's revision with some notes on nomenclature and morphology. Though variously treated in regional floras, the most significant work on *Thermopsis* since its revision has been Isely's (1981) treatment in *Leguminosae of the United States*. Isely drastically reduced the number of species in *Thermopsis*, primarily by lowering these to varietal status. He perceived variation in the western taxa as too trivial to support the specific rank. Furthermore, he saw that "all taxa are seemingly confluent with those geographically contiguous." His views were not universally accepted at the time (Turner, 1982), and our findings support recognition of most of these taxa as separate species.

*Thermopsis* is the largest and most widespread member of the small tribe Thermopsidae, which consists of about 46 species in 6 genera (Turner, 1981). All of these are restricted to temperate regions of the Northern Hemisphere. The tribe is characterized by ten free stamens and petiolate, trifoliate leaves. Though most of the genera are woody, the two herbaceous genera, *Baptisia* and *Thermopsis*, account for most of the species in the Thermopsidae. These two genera are united by many other morphological as well as secondary chemical characteristics. In fact, Larisey (1940) referred to *Thermopsis* as a western geographical supplement of *Baptisia*, though it seems more likely that one or several lines of *Baptisia* was derived from a *Thermopsis*-like ancestor (Turner, 1967). In fact, Cranmer & Turner (1967) offered *Baptisia* and *Thermopsis* as possible ancestors to the Genisteae on the basis of morphology, alkaloid chemistry, and geography. Since then, the woody Thermopsidae have been favored as close relatives to the Genisteae (Polhill, 1976; Turner, 1981).

#### BIOGEOGRAPHY

*Thermopsis* occurs not only in North America; 13 species are found in Asia. The Asian species occur at elevations of 1500–4000 m from India northward to eastern Kazakhstan and southern Russia, eastward across China, Mongolia, and Russia, and beyond to Japan, far eastern Russia, and

the North American coast of the Bering Sea. Most of the Asian species were treated by Shishkin (1945). Judging from the relative uniformity of the North American species, taxa ancestral to extant *Thermopsis* probably crossed Beringia into North America.

On the North American continent, *Thermopsis* is distributed throughout the western states and in the southern Appalachian foothills. *Thermopsis villosa* and *T. fraxinifolia* are native to Tennessee, Georgia, and the Carolinas where they occur in woodlands at elevations of 700–1600 m. Also in the east is *T. mollis*, which is found in the same states as *T. villosa* and *T. fraxinifolia* as well as in Virginia, but at lower elevations, typically between 300 and 800 m.

In western North America, *Thermopsis* occurs both in the Rocky Mountain and intermountain regions as well as in the Pacific coastal states. *Thermopsis montana* is the most widely distributed species; it is found as two intergrading, regional varieties in the intermountain region from 300 to 3200 m. Morphology and habitat are variable throughout its range from Montana southward to Arizona and New Mexico and northwestward to Wyoming, Idaho, Oregon, and Washington. Found at relatively low elevations, 1000–2000 m, is *T. rhombifolia*. Although this taxon can be found from Alberta and Saskatchewan to New Mexico, it is largely restricted to alluvial soils in dry grasslands. *Thermopsis divaricarpa* occurs at middle to high elevations, 2000–3000 m, in the Rocky Mountains from Wyoming to New Mexico, in mesophytic conifer forests.

Most of the *Thermopsis* in the Pacific coastal states is found in California. In central California, *T. californica* var. *californica* is common in chaparral west of the Sierra Nevadas up to 1000 m elevation. In northwestern California and southern Oregon, *T. gracilis* is dominant and occurs at low elevations, to 1200 m, in mesophytic forests. The remaining taxa in the extreme west have restricted distributions within California. *Thermopsis californica* var. *argentata* has a disjunct range in northeasternmost and southwestern California; this taxon grows at high elevations, 1200–2200 m, in montane chaparral and pine forests. *Thermopsis macrophylla* is known only from the western side of Santa Ynez Peak in Santa Barbara County. Our study of type material indicates that this name has been erroneously applied to the more common *T. californica* var. *californica*. Unlike the latter, *T. macrophylla* is highly localized, relatively uniform, and strikingly robust. Equally impressive in habit is *Thermopsis robusta*, which is found only in



TABLE 1. Chromosome numbers in *Thermopsis*. Counts listed with voucher only are original meiotic counts by the junior author (T); vouchers on deposit at TEX.

	2n number	Reference/voucher
Asian species		
<i>T. alterniflora</i> Regel	18	Federov (1969)
<i>T. barbata</i> Benth. ex Royle	18	Chen et al. (1992)
<i>T. chinensis</i> Benth. ex S. Moore	18	Yeh et al. (1986)
<i>T. chinensis</i> Benth. ex S. Moore	18	Chen et al. (1992)
<i>T. lanceolata</i> R. Br.	18	Mesicek & Sojak (1969)
<i>T. lanceolata</i> R. Br.	18	Chen et al. (1992)
<i>T. licentiana</i> E. Peter	18	Chen et al. (1992)
<i>T. lupinoides</i> (L.) Link [as <i>T. fabacea</i> (Pallas) DC.]	18	Federov (1969)
<i>T. lupinoides</i> (L.) Link	18	Probatova & Sokolovskaya (1981)
<i>T. mongolica</i> Czefr.	18	Mesicek & Sojak (1969)
<i>T. przewalskii</i> Czefr.	18	Chen et al. (1992)
American species		
<i>T. californica</i> var. <i>argentata</i>	18	<b>California:</b> Modoc Co., <i>T. 5813</i> , <i>T. 5816</i>
<i>T. divaricarpa</i>	36	<b>Colorado:</b> Jefferson Co., <i>T. 5636</i>
<i>T. divaricarpa</i>	36	<b>Colorado:</b> Las Animas Co., <i>T. 5772</i>
<i>T. divaricarpa</i>	36	<b>Colorado:</b> Saguache Co., <i>Tomb 649</i>
<i>T. gracilis</i>	36	<b>Oregon:</b> Lane Co., <i>T. 5797</i>
<i>T. macrophylla</i>	18	<b>California:</b> Santa Barbara Co., <i>T. 5820</i>
<i>T. montana</i> (var. <i>montana</i> ?)	18	Federov (1969)
<i>T. montana</i> (var. <i>montana</i> ?)	18	<b>Colorado:</b> Summit Co., Gillett (1975)
<i>T. montana</i> var. <i>montana</i>	18	<b>Colorado:</b> Saguache Co., <i>T. 5775</i>
<i>T. montana</i> var. <i>montana</i>	18	<b>Idaho:</b> Owyhee Co., <i>T. 5798</i>
<i>T. montana</i> var. <i>montana</i>	18	<b>Nevada:</b> Elko Co., <i>T. 5795</i> , <i>T. 5796</i>
<i>T. montana</i> var. <i>montana</i>	18	<b>Utah:</b> Wasatch Co., <i>T. 5794</i>
<i>T. rhombifolia</i>	18	CANADA: <b>Saskatchewan</b> , Ledingham (1957)
<i>T. rhombifolia</i>	18	CANADA: <b>Saskatchewan</b> , Taylor (1967)
<i>T. rhombifolia</i>	18	CANADA: <b>Saskatchewan</b> , Federov (1969)
<i>T. rhombifolia</i>	18	CANADA: <b>Manitoba</b> , Löve & Löve (1982)
<i>T. rhombifolia</i>	18	<b>Colorado:</b> Huerfano Co., <i>T. 5773</i>
<i>T. villosa</i>	18	Zhukova (1967)

Humboldt and Siskiyou Counties of northwestern California along ridgetops to 1500 m. Finally, *Thermopsis californica* var. *semota* is restricted to the woodlands of San Diego County.

#### CHROMOSOME NUMBERS

The first chromosome counts for *Thermopsis* were obtained by Russian workers in 1931 (Federov, 1969). These were obtained for the Asian species, *T. alterniflora*, and the American species, *T. montana*; both were found to have somatic counts of  $2n = 18$ . Subsequent counts for all of the species investigated have also been on a base of  $x = 9$  (Table 1).

Polyploids ( $2n = 36$ ) are known in only two species, *T. gracilis* and *T. divaricarpa*, both American, the former occurring in northern California and adjacent Oregon, the latter occurring in the front range of the Rocky Mountains, mostly in

central Colorado. Polyploidy is believed to have arisen independently in the two taxa, largely because of their geographical isolation from one another. Relatively few counts have been recorded for these two taxa, however, and it remains to be seen if such counts will hold throughout their respective distributions.

A base chromosome number of  $x = 9$  is also found in the closely related *Baptisia*, a genus of about 17 species that is confined to lower elevations of the southeastern United States (see Isely, 1981, for overview). To date, no polyploids have been reported for *Baptisia*.

#### SECONDARY CHEMISTRY (MICROMOLECULES)

Unlike in *Baptisia*, flavonoids and alkaloids have been of limited usefulness in characterizing interspecific variation in *Thermopsis*. On the basis of quinolizidine alkaloid distribution, Salatino & Gott-



lieb (1980) were able to divide *Thermopsis* into two phyletic groups, the Asian and the North American species. A comprehensive phylogeny, however, has not yet been proposed since alkaloid and flavonoid data are insufficient (Turner, 1967; Dement & Mabry, 1975) and contradictory (Balandrin et al., 1982).

Secondary chemical data have been used, nonetheless, to place the genus within a phylogenetic reconstruction of a larger scale. Based on quinolizidine alkaloid distributions (Salatino & Gottlieb, 1980), most of the Thermopsidae probably arose from "Sophora-like taxa" (Turner, 1981). Furthermore, based on serological cross reactivity of seed proteins (Cristofolini, 1987), general morphology (Polhill, 1976), and phytochemistry (Faugeras & Paris, 1968; Harborne, 1969; Salatino & Gottlieb, 1983), the woody Thermopsidae gave rise in turn to the Genisteae (Bisby, 1981; Cristofolini & Feoli-Chiapella, 1984; Polhill, 1976; Turner, 1981).

#### MORPHOLOGY

*Thermopsis* has been commonly referred to as "false lupine," "buckbean," "goldenpea," "golden banner," and "bush pea." Though the flower has inspired several of these names, it varies little within the genus and is not especially useful for specific delimitation. There are slight variations in flower size and petal shape, which often appear constant within a taxon, but these are so minor as to be of limited usefulness for identification purposes.

Fruit characters are used to distinguish between *Thermopsis* and *Baptisia*; compressed pods are mostly found in the former and inflated in the latter. The posture and shape of the mature pods vary diagnostically within *Thermopsis* as well. The fruit may be erect, ascending, or divergent from the raceme axis. There seems to be no geographical correlation to pod posture; *T. californica* and *T. macrophylla* of California, *T. montana* of the intermountain region, and *T. villosa* of the Appalachians all have erect or ascending fruits, and irregularly to strongly divergent pods are found in the remaining species. Likewise, pod shape varies among species of the same region, though pods that are strongly divergent will also be arcuate or annular. Isely (1981) noted that ovule number is characteristic within regions of the generic distribution. Indeed, we found that in southern California *Thermopsis* typically has 5–9 ovules and in northern California 8–14 ovules. The Rocky Mountain and intermountain species have 10–18 ovules and the Appalachian species have 12–16. These figures

do overlap, however, and can be called trends at best.

Vegetative characters are often quantitative with much variation around average proportions. Nevertheless, certain characters have wide diagnostic application within the genus. Plant height, leaf size and shape, and pubescence have some utility, though there is overlap between taxa, especially varieties. Although the leaf apices may differ on a single plant, the number of leaf veins and their visibility are sometimes useful. The stipules are of two types: the lower stipules in all taxa are scarious and do not subtend leaves, the upper are foliaceous and blade-bearing. The foliaceous stipules differ diagnostically in shape, ranging from lanceolate to broadly ovate, and in size, growing to 9 cm long and 6 cm wide. Inflorescence bracts, likewise, vary in shape and size and also in persistence. Racemes may bear short or long pedicels, and these may be pubescent or not. In addition, the flowers may be scattered along the axis or may be inserted in whorls, even where the flowers are not especially dense. Within the flowers, calyx proportions may confirm identity but are not especially useful alone.

Most *Thermopsis* species propagate by rhizomes, sometimes, as in *T. mollis* and *T. rhombifolia*, forming extensive clonal populations. Otherwise, the plants are supported by thick, perennial rootstocks. It is often impossible to confirm the presence of rhizomes on herbarium specimens, especially of large plants, which typically show just enough of the apical structures to fit on a herbarium sheet. Yet field observations indicate that a given taxon will have a tendency to form rhizomes or not, and this character should be preserved during collection and noted for identification.

For stems, branches, and fruits, the angle of insertion is described as erect, ascending, divergent, or spreading. Distinctions between these terms may be confusing. In the following descriptions, "erect" indicates vertical posture or nearly so and little or no curvature at the point of attachment while "ascending" indicates an angle of attachment up to 50° from vertical often with upward curvature at the point of attachment. Though "spreading" and "divergent" are roughly synonymous, here "spreading" is used for branches and "divergent" is used for fruits.

#### SPECIES AND VARIETAL CONCEPTS

As is discussed above, the primary difference in the various treatments of *Thermopsis* has been in the rank of the taxa. In this treatment, the specific rank has been chosen to express what we perceive



to be evolutionarily independent taxa. We have inferred this from morphological evidence of reproductive independence both from herbarium specimens and observations of populations in the field. For example, although occasional sympatric hybridization is suspected between members of *T. divaricarpa* and both *T. montana* and *T. rhombifolia*, there is no evidence that these hybrids have stabilized and persisted. Nevertheless, Isely occasionally, if not often, saw intergradation, where we, like Larisey, see none. We attribute the resolution of our perception to the extensive field and herbarium work that is the basis of this study.

#### TAXONOMIC TREATMENT

**Thermopsis** R. Br., Hortus Kew., ed. 2, III. 3. 1811. TYPE: *Sophora lupinoides* L. = *Thermopsis lanceolata* R. Br. = *Thermopsis lupinoides* (L.) Link.

*Thermia* Nutt., Gen. N. Amer. Pl. 1: 282. 1818. TYPE: *Thermia rhombifolia* (Pursh) Nutt.

*Scolobus* Raf., Amer. Monthly Mag. Crit. Rev. 4: 193. 1819. TYPE: *Scolobus rhombifolius* (Nutt. ex Pursh) Raf.

*Drepilia* Raf., N. Fl. 2: 52. 1836 [1837]. TYPE: *Drepilia rhombifolia* (Nutt. ex Pursh) Raf.

Perennial herbs, usually rhizomatous; stems erect or ascending, few-branched to well-branched, branches ascending or spreading; plants glabrate to variously pubescent, unarmed. Leaves petiolate, trifoliolate, not glandular-punctate; stipules usually persistent, foliaceous or nearly so, dimorphic, the lowermost amplexicaul, scarious, and not blade-bearing, the rest broadly ovate to lanceolate and subtending leaves, to 6(-9) cm long, to 3(-6) cm wide, smaller and narrower on branches; leaflets subpetiolulate, narrowly elliptic to obovate, 2-8(-10) cm long, margins entire; estipellate. Inflorescences terminal (lateral) racemes, commonly solitary, flowers few to numerous, scattered or whorled; bracts deciduous or persistent, widely ovate to lanceolate, acute to acuminate; bracteoles ab-

sent; pedicels 2-17 mm long. Flowers papilionaceous; calyx campanulate, appearing 4-lobed, subequal, the upper lobe double, broader, and slightly longer than the others, truncate to emarginate, the lower lobes deltoid to lanceolate; corolla yellow; banner very widely ovate, shorter than wings and keel, cleft (emarginate and short mucronate), claw cuneate to oblong, replicate-reflexed; wings usually asymmetric, elliptic to oblong-rhombic, auriculate,  $\pm$  length of keel, not adnate to keel, claw narrowly oblong; keel asymmetrically oblong-elliptic to carinate, auriculate, posteriorly fused, without a beak, claw narrowly oblong; stamens 10, free, uniform; anthers dorsifixed; pistil short-stipitate; ovary oblong, usually longer than style, villosulous; ovules 5-15; style glabrous; stigma minute. Legumes persistent, erect, ascending, or divergent, tan to brown, narrowly elliptic, laterally compressed, straight, arcuate, or rarely annular, margins straight or, as a consequence of ovule abortion, sinuate or lomentaceous; pericarp chartaceous, not elastic, variously pubescent; stipe 2-4 mm long; fruits slowly dehiscent, valves separating from apex through both sutures. Seeds (1-)3-10 per fruit, tan to brown-black, oblong to reniform, often with a minute, membranaceous rim-aril. Base chromosome number,  $x = 9$ .

*Diagnosis and relationships.* *Thermopsis* is a member of the Thermopsidae Yakovlev (Bot. Žurn. 57: 585-595, 1972), by virtue of its free stamens and palmately trifoliolate, petiolate leaves. Although *Thermopsis* is loosely allied with all other Thermopsidae, it is very similar morphologically to *Baptisia*, the other prominent North American member of the tribe. Fruiting *Thermopsis* can be distinguished readily from *Baptisia*. The pods of North American *Thermopsis* are flattened, while those of *Baptisia* are inflated.

As detailed above, *Thermopsis* is found in Asia and North America. In North America four species occur in the Pacific coastal states, three occur in the Rocky Mountains and intermountain regions, and three are found in the southern Appalachians.

#### KEY TO SPECIES

- 1a. Plants of southern Appalachian foothills.
  - 2a. Stipules on primary axis more than 1 cm wide; pedicels less than 3 mm long; pods erect, densely villous ..... 10. *Thermopsis villosa*
  - 2b. Stipules on primary axis less than 1 cm wide; pedicels more than 3 mm long; pods irregularly divergent, pubescent or glabrate.
    - 3a. Plants rhizomatous; pedicels villosulous and shorter than bracts; racemes terminal; mostly piedmont, 300-800 m ..... 6. *Thermopsis mollis*
    - 3b. Plants from a single woody rootstock; pedicels glabrate and at least as long as bracts; racemes terminal or lateral; montane, usually 1000-2000 m ..... 3. *Thermopsis fraxinifolia*
- 1b. Plants of Rocky Mountains, intermountain regions, and Pacific coastal states.
  - 4a. Plants tomentose or sericeous throughout; flowers usually in whorls of 3-5; California.



- 5a. Plants mostly 3–8 dm tall; leaflets mostly 3–7 cm long; pods ascending, usually with several or more abortive ovules ..... 1. *Thermopsis californica*
- 5b. Plants mostly 10–20 dm tall; leaflets up to 11 cm long; pods ascending or divergent, usually with well-developed ovules.
  - 6a. Pods ascending and straight; pedicels 2.5–4 mm long; lateral leaf veins 6–8 pairs; Santa Ynez Mts. of California ..... 5. *Thermopsis macrophylla*
  - 6b. Pods divergent and arcuate; pedicels 4–8 mm long; lateral leaf veins 9–12 pairs; Humboldt and Siskiyou Counties of northwestern California ..... 9. *Thermopsis robusta*
- 4b. Plants glabrate to pubescent; flowers usually scattered; Pacific coastal mountains north of 40°N latitude, and more central portions of the western United States and adjacent Canada.
  - 7a. Pods erect and straight ..... 7. *Thermopsis montana*
  - 7b. Pods divergent and straight, arcuate, or annular.
    - 8a. Branches spreading, strongly zigzagged; leaflets more than 2 cm wide, sometimes emarginate; petioles more than 2.5 cm long; pods straight; western Oregon and northern California ..... 4. *Thermopsis gracilis*
    - 8b. Branches ascending, weakly to moderately zigzagged; leaflets less than 2 cm wide, not emarginate; petioles less than 2.5 cm long; pods usually arcuate or annular; northern and eastern Rocky Mountains and adjacent Great Plains.
      - 9a. Plants 3–9 dm tall; leaflets more than 3 cm long, lateral veins 7–10 pairs; stipules ovate to narrowly elliptic; flowers 2.5–3.0 cm long; pods straight to arcuate ..... 2. *Thermopsis divaricarpa*
      - 9b. Plants mostly 1–3 dm tall; leaflets less than 3 cm long, lateral veins 5–7 pairs; stipules usually widely ovate; flowers 1.6–2.1 cm long; pods strongly arcuate to annular ..... 8. *Thermopsis rhombifolia*

**1. *Thermopsis californica*** S. Watson, Proc. Amer. Acad. Arts 11: 126. 1876. TYPE: U.S.A. California: Marin Co., Corte Madera, *J. M. Bigelow* 1854 (lectotype, selected here, NY; probable isoelectotypes, NY, PH, US).

Plants robust, (2.5)3–8 dm tall, sericeous or tomentose; stems slender, erect, clustered, well-branched, arising from rhizomes; branches ascending at 20–45°, weakly to strongly zigzagged. Leaflets elliptic or obovate, 3–7(–9) cm long, 1.2–4(–4.5) cm wide, obtuse or acute, silvery sericeous or tomentose to villous, lateral veins 6–9 pairs, conspicuously net-veined beneath; petioles 1–3.5 cm long; stipules persistent, widely ovate to lanceolate, 1.5–6.5 cm long, 0.7–5 cm wide, cuneate to amplexicaul, acuminate. Racemes 7–30(–35) cm long, with 10–40 flowers usually in whorls of 3–5; peduncles (2–)4–10 cm long; pedicels 2–6 mm long, sericeous or tomentose; bracts semipersistent, ovate to lanceolate, 6–15 mm long, 2.5–15(–20) mm wide. Flowers 1.5–2.0 cm long; calyx 5–10 mm long, 5–9 mm wide at the limb, lobes 2.5–5 mm long, as long or longer than tube; wing and keel petals oblong-elliptic to nearly reniform; ovary velutinous; ovules 5–11. Pods straight, ascending (irregularly divergent when young), 2–6(–7) cm long, (0.5–)0.6–0.9 cm wide, sericeous, tomentose, or velutinous. Seeds 1–6(–10), oblong with a short rostrum, 4–5.5 mm long, 2.5–4 mm wide.

Three varieties are recognized within *Thermopsis californica* as follows:

KEY TO VARIETIES OF *THERMOPSIS CALIFORNICA*

- 1a. Stipules widely ovate to ovate, to 5.0 cm wide; bracts to 15 mm wide; peduncles usually more than 6 cm long; pod pubescence of matted trichomes ..... 1b. *Thermopsis californica* var. *californica*
- 1b. Stipules ovate to lanceolate, to 2.5 cm wide; bracts to 6 mm wide; peduncles usually less than 6 mm long; pod pubescence of straight, appressed trichomes.
  - 2a. Silvery sericeous throughout; wing and keel petals reniform; northeastern and southwestern California ..... 1a. *Thermopsis californica* var. *argentata*
  - 2b. Villous to densely tomentose; wing and keel petals oblong-elliptic; restricted to San Diego Co., California ..... 1c. *Thermopsis californica* var. *semota*

**1a. *Thermopsis californica* var. *argentata*** (E. Greene) C. J. Chen & B. Turner, comb. nov. Basionym: *Thermopsis argentata* E. Greene, Erythea 3: 18. 1895. *Thermopsis gracilis* var. *argentata* (E. Greene) Jepson, Man. Fl. Pl. Calif. 515. 1925. *Thermopsis macrophylla* var. *argentata* (E. Greene) Jepson, Man. Fl. Pl. Calif. 2: 245. 1936. TYPE: U.S.A. California: Modoc Co., “Forestdale,” *Baker* 1893 (lectotype, selected here, ND; isoelectotypes, CAS, ND, NY, US).

In his protologue Greene cited a single collection from Modoc County, without locality, made by Milo S. Baker in 1893. Examination of material at ND reveals two sheets collected by Baker in the “Big Valley Mts.” during June–August 1893. Both



sheets, which bear printed labels, were subsequently modified by hand-inkings so as to read August 1894. One sheet is clearly a mixture of plants collected in June (flowering sprig) and fall (late fruiting sprig). The other sheet is in late fruit. We have designated the latter as lectotype.

Plants (2.5–)3–5 dm tall, silvery sericeous throughout; branches weakly to moderately zigzagged. Leaflets obovate to elliptic, 3–6.5 cm long, 1.2–3.5 cm wide, obtuse to acute sometimes with a short mucro; petioles 1.3–2.1 cm long; stipules lanceolate to ovate, 1.5–6.0 cm long, 0.8–2.5 cm wide, cuneate to cordate. Racemes 8–20(–25) cm long, with 10–30 flowers; peduncles 4–7(–10) cm long; bracts ovate to lanceolate, 7–15 mm long, 2.5–5 mm wide. Calyx 7–9(–10) mm long, 5–8 mm wide at the limb, lobes 3.5–4.5(–5) mm long; banner cleft; wing and keel petals asymmetrically oblong-elliptic to reniform; ovules 8–11. Pods 3–6(–7) cm long, (0.5–)0.7–0.9 cm wide. Seeds 1–6, oblong, 4–5(–5.5) mm long, (2.5–)3.5–4 mm wide. Chromosome number,  $2n = 18$ .

*Distribution and ecology* (Fig. 1). Northeasternmost California (southeastern Siskiyou Co. and closely adjacent Shasta, Modoc, and Lassen cos.) and again in southwestern California (Kern, Ventura, Santa Barbara, and Los Angeles cos.), mostly interior montane chaparral and pine forests from 1200 to 2200 m; flowering May–June.

*Representative specimens examined.* U.S.A. **California:** Kern Co., Mt. Pinos, June 1905, *Hall* 6378 (UC); Owens Valley and at Fort Tejon, *Horn* 1863 (NY). Lassen Co., ridge W of Nubieber, along California Hwy. 299, 26 June 1941, *Heller* 16229 (MO, NY, WTU). Los Angeles Co., Santa Barbara, Liebre Ridge, N slope Liebre Mt., 15 Oct. 1923, *Hunt* 5 (CAS, RM). Modoc Co., Forestdale, *Baker* 1894 (NY, PH, POM, RM, US); Forestdale, *Baker* 1899 (PH, UC); Forestdale, *Baker & Nutting* 1894 (CAS, GH, NY, RM, UC); 3 mi. NW of Lookout, 3 June 1968, *Turner* 5813 (TEX); 14 mi. NW of Lookout, 3 June 1968, *Turner* 5816 (TEX). Santa Barbara Co., San Rafael Mt., *Ford* 1887 (GH); Santa Ynez, Big Pine Mt., 7 Aug. 1936, *Peterson* 303 (UC). Shasta Co., ca. 20 mi. W of Fall River Mills, 24 May 1940, *Hitchcock* 6533 (NY, POM, UC, WTU); 1 mi. W of Dana, 2 June 1968, *Turner* 5809 (TEX). Siskiyou Co., just E of Barnum Flat Reservoir, 3 June 1968, *Turner* 5817 (TEX). Ventura Co., Fort Tejon, 19 June 1935, *Axelrod* 434 (POM, UC); Mt. Pinos region, 28 June 1896, *Dudley & Lamb* 4745 (CAS, UC); Lakes Ridge, above Maricopa Road on Matilija-Sespe divide, *Pollard* 1955 (CAS, COLO, TEX); 0.25 mi. NW of Reyes Peak, 23 Apr. 1934, *Sowder* 393 (UC).

*Thermopsis californica* var. *argentata* differs from the more widespread, more variable variety

*californica* in its smaller habit and closely appressed, silvery vestiture.

We are unable to distinguish between the northern and southern populations (Fig. 1). Isely (1981) applied the varietal name *argentata* (as part of his *T. macrophylla*) only to the more northern populations and included the southern populations in his *T. macrophylla* var. *macrophylla*. We agree with the assessment of Abrams (1944) that these disjunct interior populations represent a single taxon. At least we can find no characters by which to distinguish them though both are readily distinguished from varieties *californica* and *semota* by habit, vestiture, and petal shape.

#### 1b. *Thermopsis californica* var. *californica*.

*Thermopsis californica* var. *velutina* E. Greene, *Erythea* 1: 81. 1893. *Thermopsis velutina* (E. Greene) E. Greene, *Erythea* 3: 19. 1895. *Thermopsis gracilis* var. *velutina* (E. Greene) Jepson, *Man. Fl. Pl. Calif.* 515. 1925. *Thermopsis macrophylla* var. *velutina* (E. Greene) Larisey, *Ann. Missouri Bot. Gard.* 27: 256. 1940. TYPE: U.S.A. California: Santa Clara Co., Mount Hamilton, *Greene* 1891 (lectotype, selected here, ND; isolectotype, ND).

In his protologue Watson did not cite specimens, but rather referred to the species as occurring in "Marin and Napa Counties, California, and probably southward." He did say that his *Thermopsis californica* was the same as what Torrey had referred to as "*T. macrophylla*" (Torrey, 1857) and *T. "fabacea"* (Torrey, 1859). Watson, in his protologue, indirectly suggested a lectotype with his citation of the Pacific Railroad Report in which Torrey cited a Bigelow collection from "Corte Madera," which is located in Marin County, California. We have selected the Bigelow collection from among contending lectotypes since the Torrey Herbarium collection at NY has the name *Thermopsis californica* Watson written on it, presumably in Watson's hand. Duplicates of the Bigelow collections were not found at GH, where Watson worked, nor were other contending lectotype collections annotated by him as belonging to *Thermopsis californica*.

Plants 3–8(–9) dm tall, sparsely to densely tomentose or villous; branches weakly to moderately zigzagged. Leaflets elliptic to obovate or rhombic, 3.5–7(–9) cm long, 2–4(–4.5) cm wide, obtuse to acute; petioles 1.5–3.5 cm long; stipules widely ovate to narrowly ovate, 2.5–6.5 cm long, 1.5–5.0 cm wide, cuneate to amplexicaul. Racemes



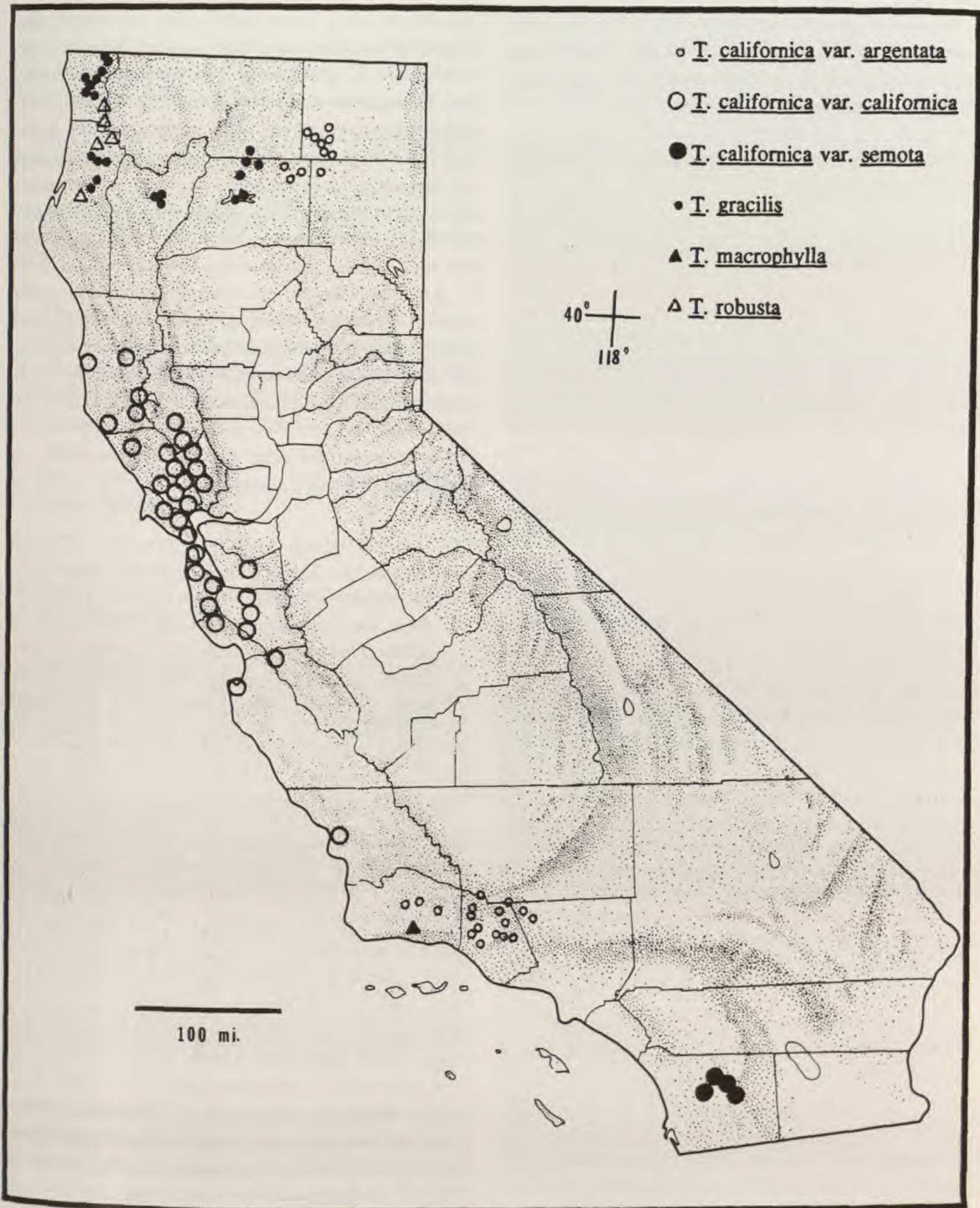


FIGURE 1. Distribution of *Thermopsis* in California: *T. californica* var. *argentata* (small open circles); *T. californica* var. *californica* (large open circles); *T. californica* var. *semota* (large closed circles); *T. gracilis* (small closed circles); *T. macrophylla* (closed triangle); *T. robusta* (open triangle).

10-30(-35) cm long, with 12-40 flowers; peduncles (4-)6-10 cm long; bracts widely ovate to nearly lanceolate, 6-15(-30) mm long, 3-15(-20) mm wide. Calyx 5-8(-9) mm long, 6-9 mm wide

at the limb, lobes 2.5-5 mm long; banner cleft; wing and keel petals asymmetrically oblong-elliptic; ovules 5-8. Pods 3-5.5 cm long, 0.6-0.7 cm wide. Seeds 3-5(-10), oblong, 4 mm long, 2.8 mm wide.



*Distribution and ecology* (Fig. 1). Coastal regions of central California from 35 to 40°N latitude, mostly chaparral from near sea level to about 1000 m; flowering May–June.

*Representative specimens examined.* U.S.A. **California:** Alameda Co., hills E of Oakland, 1 Apr. 1929, *Tebbe 62* (UC). Lake Co., 9 mi. from Lower Lake on Monticello Road, 23 May 1937, *Ewan 10352* (COLO, MO, NY); flats near Morgan Valley, 25 May 1920, *Jepson 9034* (JEPS). Marin Co., Sausalito to Larkspur, 27 Apr. 1918, *Abrams 6882* (CAS, NY, US); San Rafael, dry hillsides, *Bolander 1860–1867* (F, MO); Angel Island, San Francisco Bay, *Chestnut 1888* (F, UC, US); Lagunitas, *Grinnell 1918* (CAS, MO, NY, RM, UC); Tiburon, 17 Apr. 1938, *Rose 38146* (GH, MO, NY, WTU, UC). Mendocino Co., 5 mi. E of Point Arena, 29 May 1939, *Rose 39184* (GH, MO, NY, UC, US); Little Lake Valley 2.5 mi. SE of Willits, *Wiggins & Ferris 10183* (CAS, RM, TEX, WS, WTU). Monterey Co., hill near Monterey, 13 June 1861, *Brewer 704* (UC, US). Napa Co., Knoxville, 8 May 1903, *Baker 3081* (F, GH, LL, MO, NY, UC); 5 mi. S of Calistoga, 12 Apr. 1924, *Heller 13837* (CAS, F, MO, NY, US). San Benito Co., Aromas, *Hickman 1915* (CAS, GH, US). San Luis Obispo Co., along old road to Pozo, 17 May 1928, *Eastwood 15140* (CAS, UC); San Luis Obispo, 9 May 1882, *Jones 2660* (CAS, MO, NY, PH, RM, UC). San Mateo Co., Crystal Springs Lake, May 1903, *Elmer 4824* (ARIZ, CAS, MO, NY, OSC, UC, US, WS); Crystal Springs Lake, 1 May 1902, *Greene 685* (CAS, GH, LL, MO, NY, UC, US, WTU); Mt. Hamilton, June 1903, *Elmer 5023* (ARIZ, CAS, MO, NY, UC, WS); Smith Creek, foot of Mt. Hamilton, 10 May 1907, *Heller 8518* (CAS, GH, F, MO, NY, PH, UC, US, WTU); trail to Pine Ridge, N of Madrone Springs, 29 May 1895, *Smith 4075* (GH, OSC, RM, TEX). Santa Cruz Co., Glenwood, *Davis 1907* (CAS, GH, RM, UC, US); Bear Creek Road about 3 mi. E of Boulder Creek, 18 May 1946, *Ferris 11130* (CAS, GH, RM, TEX, UT, WS). Sonoma Co., between Santa Rosa and Agua Caliente, 22 Apr. 1902, *Heller & Brown 5343* (CAS, COLO, GH, MO, NY, RM, US); 6.8 mi. E of Santa Rosa on road to Calistoga, 30 Apr. 1949, *Wiggins 12058* (CAS, UC, WTU).

This is the more commonly encountered, more variable taxon of the *Thermopsis californica* complex. It is distinguished from both *T. californica* var. *semota* and *T. californica* var. *argentata* by its larger habit, broader stipules and bracts, and sparsely to densely tomentose vestiture.

Brewer & Watson (1880) correctly noted that *Thermopsis macrophylla* is distinct from *T. californica*. Nevertheless, most workers have treated these taxa as synonymous with the earlier name, *Thermopsis macrophylla*. We view *T. macrophylla*, like Brewer & Watson, as a localized endemic that is restricted to the Santa Ynez Mountains near Santa Barbara, California. Collections of *Thermopsis californica* are not sympatric and do not intergrade with *T. macrophylla*. Isely (1981), who treated *T. californica* var. *californica* within

his concept of *T. macrophylla* var. *macrophylla*, perceived “a cline towards [*T. macrophylla*] var. *venosa* [= *T. gracilis* in the present treatment] that characteristically has spreading and (comparatively) narrow fruits.” This statement was qualified by the remark that “few specimens possess mature pods.” Examination of many diverse specimens from northern California shows that the geographical hiatus shown by Isely in mapping the two taxa is real, and that the few collections of his *T. macrophylla* var. *macrophylla* that he maps within the range of *T. gracilis* (of the present treatment) are mostly nonfruiting forms of *T. gracilis* that are otherwise superficially similar to *T. macrophylla* var. *macrophylla* (sensu Isely). We do not see any evidence of clinal intergradation between these two taxa, nor do they co-occur, as suggested in Isely’s treatment.

**1c. *Thermopsis californica* var. *semota*** (Jepson) C. J. Chen & B. Turner, comb. nov.  
Basionym: *Thermopsis macrophylla* Hook. & Arn. var. *semota* Jepson, Fl. Calif. 2: 245. 1936. *Thermopsis macrophylla* Hook. & Arn. subsp. *semota* (Jepson) Beauchamp, Phytologia 59: 439. 1986. TYPE: U.S.A. California: San Diego Co., Spencer Valley, vicinity of Julian, *Alderson 1898* (holotype, UC).

Plants 3–5(–6) dm tall, densely silvery tomentose; branches moderately to strongly zigzagged. Leaflets elliptic to narrowly elliptic, 3–6.5(–7.5) cm long, 1.2–3.5(–3.8) cm wide, acute to obtuse with a short mucro; petioles 1–2 cm long; stipules ovate to lanceolate, 1.5–5.5 cm long, 0.7–2.4 cm wide, cuneate to cordate. Racemes 7–20(–30) cm long, with 10–30 flowers; peduncles 2–6(–9) cm long; bracts ovate to nearly lanceolate, 6–11 mm long, 3.5–6 mm wide. Calyx 5–8(–9) mm long, 5–8 mm wide at the limb, lobes 3–5 mm long; banner shallowly emarginate and short mucronate; wing and keel petals asymmetrically oblong-elliptic; ovules 5–7. Pods 2–4 cm long, 0.6–0.7 cm wide. Seeds 1–2 (fully matured not seen).

*Distribution and ecology* (Fig. 1). Interior portions of San Diego Co., California, grassy oak woodlands, 1000–1500 m; flowering April–June.

*Representative specimens examined.* U.S.A. **California:** San Diego Co., 1.7 mi. NW of Julian, 5 Apr. 1957, *Bacigalupi et al. 5799* (JEPS, RM, WTU); near Julian, *Epling 1932* (CAS, NY, POM, UC); Cuyamaca Reservoir, 5 June 1946, *Fiker 3576* (RM, UC, WS); Julian, Cuyamaca Mts., 28 May 1899, *Hall 1205* (CAS, NY, UC); vicinity of Santa Ysabel, *Henshaw 1893* (US);



Laguna Mts., 25 June 1924, *Munz 8377* (GH, NY, POM); Pine Hills, 1 June 1917, *Spencer 504* (GH, NY, POM, UC); Ramona, head of Cedar Creek, 27 Mar. 1934, *Wieslander 447* (UC).

Isely (1981) treated this taxon as a localized variety within his concept of *Thermopsis macrophylla*. We agree with his circumscription. Larisey (1940) inexplicably omitted the taxon from her treatment.

2. ***Thermopsis divaricarpa*** Nelson, Bot. Gaz. 25: 275. 1898. *Thermopsis rhombifolia* var. *divaricarpa* (Nelson) Isely, Brittonia 30: 470. 1978. TYPE: U.S.A. Wyoming: Albany Co., Johnson's ranch, Big Laramie River, 8 Aug. 1897, *A. Nelson 3903* (lectotype, selected here, RM; isolectotypes, GH, NY [dated 7 Aug. 1897], RM).

*Thermopsis pinetorum* E. Greene, Pittonia 4: 138. 1900. TYPE: U.S.A. Colorado: Saguache Co., below Marshall Pass, *Greene 1896* (lectotype, selected here, ND; isolectotype, ND).

Two different collections of *Thermopsis divaricarpa*, *E. Nelson 3424* (Pole Creek, 22 July 1897) and *A. Nelson 3903*, were designated as "type specimens" by A. Nelson, without indication of the holotype. Isely (1978) designated *Nelson 3903* as the "holotype"; he should have designated this as a lectotype.

In his protologue for *Thermopsis pinetorum*, Greene cited collections made by himself "in fruit, below Marshall Pass," 4 Sep. 1896 and collections by C. F. Baker at Los Pinos (which is near Bayfield in La Plata Co.), 23 May 1899, in flower. The latter collections appear to belong to *Thermopsis montana*. The former is selected as the lectotype since mature fruits best serve to distinguish between the taxa concerned.

Plants delicate, 3–6(–9) dm tall, glabrate or puberulent; stems slender, erect, clustered, moderately branched, arising from a thick woody rootstock or rhizomes; branches ascending at 20–35°, moderately to strongly zigzagged. Leaflets elliptic to narrowly elliptic or rhombic, 3–7 cm long, 0.5–2.5 cm wide, acute to obtuse, glabrate to puberulent, lateral veins 7–10 pairs, conspicuously net-veined beneath; petioles 1–2.5 cm long; stipules persistent, ovate to narrowly elliptic, 2–3.5(–4) cm long, 0.7–3 cm wide, cuneate to cordate, acute. Racemes 7–15 cm long, with 5–15 flowers, usually in whorls of 2–4; peduncles 3–5 cm long; pedicels 5–8 mm long, glabrate to puberulent; bracts deciduous, ovate to lanceolate, 7–14 mm long, 3–5

mm wide. Flowers 2.5–2.9 cm long; calyx 8–11 mm long, 6–8 mm wide at the limb, lobes 2–5 mm long, as long as or shorter than tube; wing and keel petals elliptic to asymmetrically oblong-elliptic; ovary appressed pubescent; ovules 10–18. Pods straight to arcuate to ca. 45°, divergent, 6.5–9 cm long, 0.6–0.8 cm wide, inconspicuously appressed pubescent. Seeds (6–)10–14, brown-black, elliptic with a rostrum, 4–5 mm long, 2–2.5 mm wide. Chromosome number,  $2n = 36$ .

*Distribution and ecology* (Fig. 2). South-central Wyoming (mainly Albany Co.) southeastward through the front range of the Rocky Mountains to northeasternmost New Mexico, mostly pine or spruce forests, usually along streams or in moist open areas, 2000–3000 m; flowering (April–)May–June(–July).

*Representative specimens examined*. U.S.A. **Colorado**: Alamosa Co., near S entrance of Great Sand Dunes National Monument, 18 May 1969, *Dennam 2950* (TENN). Boulder Co., Boulder, 21 Aug. 1884, *Letterman 141* (MO, US); plains and foothills near Boulder, July 1902, *Tweedy 5158* (NY, RM). Chaffee Co., Salida, 18 May 1925, *Nelson 10495* (NY); Salida, 7–8 Oct. 1918, *Eggleston 15019* (US). Clear Creek Co., Idaho Springs, rocky hillsides, 15 May 1916, *Clokey 2676* (RM, UC); Chicago Creek, 11 July 1942, *Ehlers 8398* (COLO, TEX); Empire, 2,576 m, 15–25 July 1903, *Tweedy 5652* (NY, RM). Costilla Co., mountain near La Veta Pass, 20 June 1900, *Rydberg & Vreeland 5935* (NY). Custer Co., North Creek Campground, 30 May 1954, *Douglass 58* (COLO); Sangre de Cristo Creek, 2 July 1900, *Rydberg & Vreeland 5933* (NY, RM). Douglas Co., along Colorado Hwy. 67, 8.3 mi. N of junction of Colorado Hwy. 67 and County Road 126, 18 May 1987, *Falb & Miercort 113* (RM). El Paso Co., Colorado Springs, *Jones 1879* (ARIZ, NY, US); near Palmer Lake, 21 June 1936, *Rollins 1187* (GH, MO, ND, NY); Garden of the Gods, *Schallert 1943* (F, NY, PH, WS). Fremont Co., near Hillside, 4 June 1949, *Gates 22053* (TEX). Garfield Co., White River, Grizzly Creek, 26 June 1932, *Ware 24* (RM); 38.8 mi. S of junction Colorado Hwy. 64 on Colorado Hwy. 139, 14 June 1971, *Wofford 1-77* (TENN). Gilpin Co., near summit of Black Hawk Pass, *Alston 1964* (TEX); Tolland, *Overholts 1913* (MO, NY). Grand Co., Trail Ridge Road, 11.5 mi. N of Grand Lake, 21 July 1961, *Douglass 320* (TEX); Hot Sulphur Springs, 30 May 1940, *Pohl 1954* (PH). Huerfano Co., 8 mi. SW of Cuchara, Bear Lake Camp, 4 Aug. 1970, *Stephens & Brooks 42675* (NY, UC); Erwind Canyon, W of Walsenburg, 14 June 1941, *A. & R. A. Nelson 4595* (RM). Jackson Co., Gould Ranger Station, 23 Sep. 1944, *Ginter 891* (RM). Jefferson Co., Vernon Canyon, 20 June 1921, *Bethel & Clokey 4186* (CAS, COLO, F, MO, NY, PH, POM, RM, UC, US); near Golden, Guy Hill, 2 June 1938, *Ehlers 6850* (ARIZ, GH, NCU, ND, PH); ca. 11 mi. W of Littleton, 20 May 1967, *Turner 5637* (CAS, RM, TEX). Lake Co., Everett, 7 May 1919, *Clokey 3588* (CAS, F, GH, MO, POM, RM, TEX, US). Larimer Co., Estes Park, May 1895, *Baker 2581* (COLO, MO, NCU, WS). Las Animas Co., 11 mi. N of Stonewall, 26 May 1968, *Turner 5772* (TEX). Mesa Co., 13 Aug. 1981, *Siplivinsky 1961*



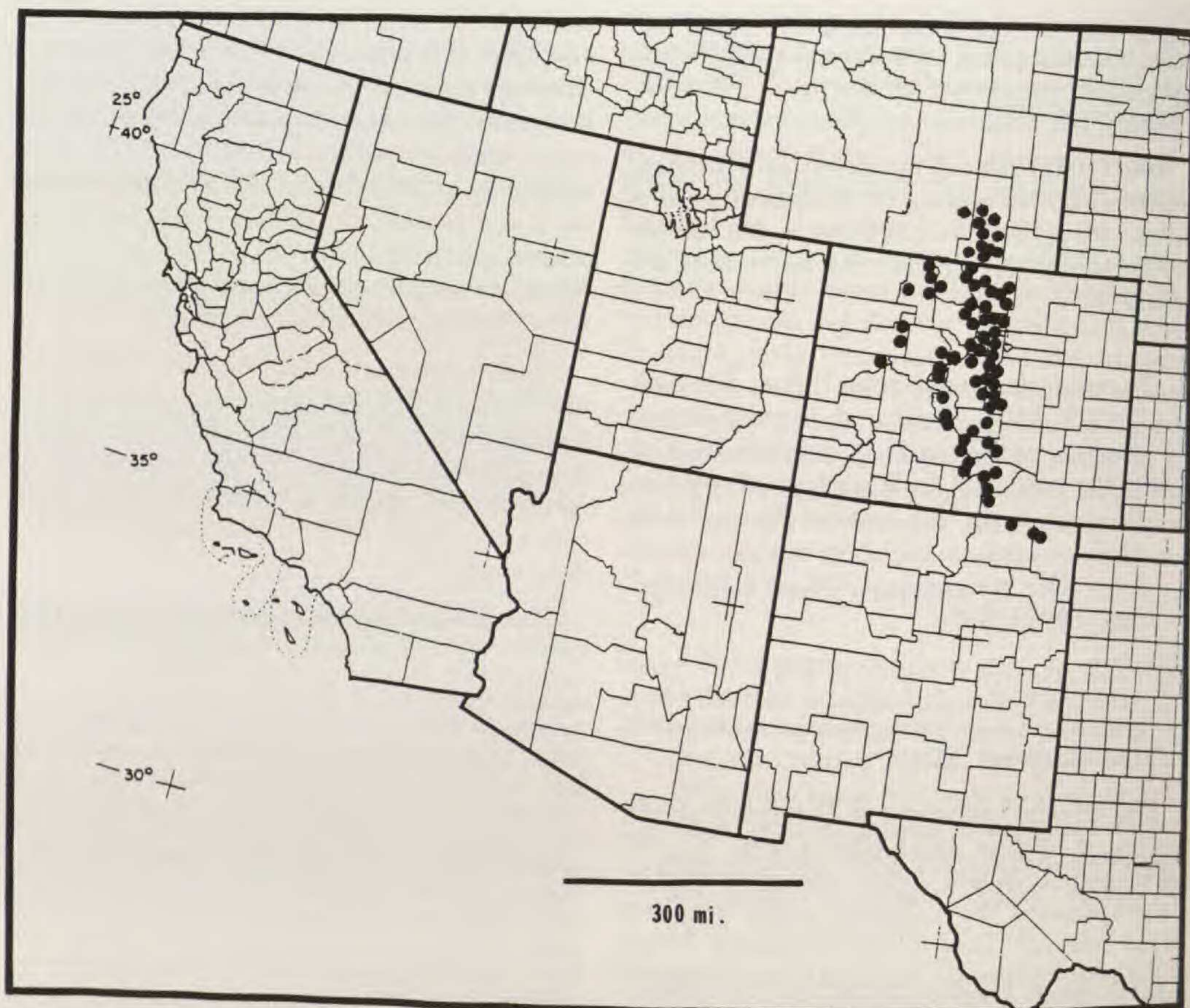


FIGURE 2. Distribution of *Thermopsis divaricarpa*.

(COLO). Park Co., Pine Junction to Wandcrest Park, 27 June 1971, *Kathleen & Shea 65* (MO); near Jefferson, Michigan Creek drainage, 16 July 1960, *Walter 369* (COLO). Pueblo Co., near Beulah, 6 June 1908, *Robbins 4991* (COLO); W of Pueblo, 8 May 1908, *Robbins 4991* (COLO). Routt Co., Elkhead Mts., 10 July 1988, *Flock 2004* (COLO, RM); Anita Peak, 3 Aug. 1903, *Goodding 779* (CAS, COLO, GH, MO, NY, PH, RM, UC, US). Saguache Co., Marshall Pass, 19 July 1901, *Baker 485* (F, MO, NY, RM, UC, US); 8 mi. E of Marshall Pass, 27 May 1968, *Turner 5776* (TEX). Summit Co., near Breckenridge, *Mackenzie 256* (MO, NY, RM, UC); near Bear River, 30 June 1926, *Payson 4833* (GH). Teller Co., S side of Lower Twin Rocks Road, 10 June 1987, *Barzee et al. 717* (COLO); 6 mi. NNW of Woodland Park, *Devender & Kearns 1977* (ARIZ). **New Mexico:** Colfax Co., Cimarron Pass, 28 May 1934, *McKelvey 2405* (GH); Raton, 10 June 1887, *Evans 59* (NY). Union Co., Sierra Grande, 19 June 1911, *Standley 6140* (US); 7 mi. S of Des Moines, 14 May 1974, *Stephens 75588* (NY). **Wyoming:** Albany Co., Vedauwoo Hills E of Laramie, 13 June 1940, *Cain 65* (MO, TENN); Little Laramie River, 15 June 1901, *Goodding 10* (CAS, F, GH, MO, NY, POM, RM, UC, US, UT); Rock River, 30 June 1914, *Macbride 2403* (RM, WS); Big Laramie River, 5 July 1900, *Nelson 271* (GH, NY, RM); Sand Creek, 2 June 1900, *Nelson 7031* (CAS, COLO, GH, MO, NY,

POM, RM, UC, US); Mandel, 24 July 1903, *Nelson 8910* (COLO, GH, MO, NY, UC); Fish Creek, 4 July 1917, *Nelson 9784* (GH, MO, RM, TENN, UC); Pole Mt. region, 6 July 1943, *Porter 3245* (CAS, GH, MO, NY, UC, US, WTU); Crow Creek, Laramie Hills, 11 July 1935, *Rollins 977* (GH, MO, NY, WS); Laramie River near Laramie, 16 June 1935, *Williams 2214* (GH, MO, UC, US); near Crow Creek, Laramie Mts., 20 June 1935, *Williams 2236* (GH, MO, UC, WS). Carbon Co., McFadden, in Medicine Bow Mts., 13 June 1972, *Jones 1085* (MO).

Isely (1981) treated this taxon within his broad concept of *Thermopsis rhombifolia*, noting that it stands morphologically and geographically somewhat between *T. rhombifolia* and *T. montana*, which it does. Nevertheless, we have retained *T. divaricarpa* as a distinct species.

We have found that *T. rhombifolia*, *T. divaricarpa*, and *T. montana* are clearly distinct throughout most of their ranges and do not appear to intergrade as do the varieties in the *Thermopsis montana* complex. Indeed, in Colorado where the several taxa are partially sympatric, *T. rhombifolia*



occurs mostly at lower elevations in deeper and drier alluvial soils, *T. divaricarpa* at mid-elevations in mesophytic habitats, and *T. montana* at higher, subalpine elevations.

It is true, however, that occasional intermediates between *Thermopsis divaricarpa* and *T. rhombifolia* occur, but we view such variation as derived from relatively isolated hybridization events. Such "hybridized" populations occur in Albany County, Wyoming, and probably occasioned the description of *T. arenosa*, which appears to combine some of the features of *T. divaricarpa* in the genetic backdrop of *T. rhombifolia*. Likewise, in Colorado at Marshall Pass along the Saguache-Chaffee county line, *T. montana* and *T. divaricarpa* occur in close proximity and there has apparently been some gene exchange between the two. The variants from this region have the general habit of *T. divaricarpa*, but the ascending pods approach those of *T. montana*. The form may have precipitated the description of *T. pinetorum*. The third author visited the general area of the type locality of *T. pinetorum* in May 1968 (Turner 5776, TEX) and again in July 1991, and was impressed by the populational variation in that vicinity, especially along the eastern slopes leading to Marshall Pass. But such morphological aberrations are mere wrinkles in the broad distributional fabric of *T. rhombifolia*, *T. divaricarpa*, and *T. montana* and do not make a case for their taxonomic submergence. If it were so, then many distinct species among the closely related genus *Baptisia* would be merged, for occasional or even rampant hybridization is the rule when species of these taxa occur together (under disturbance). Indeed, interspecific hybridization between the closely related taxa *T. rhombifolia*, *T. divaricarpa*, and *T. montana* is apparently much less common than among the more distantly related (among themselves) species, *Baptisia leucophaea*, *B. sphaerocarpa*, and *B. leucantha* (Alston & Turner, 1963).

It is indeed likely, however, that *T. divaricarpa* had an amphiploid origin from *T. rhombifolia* and *T. montana*. So far as is known, *T. divaricarpa* is tetraploid with  $2n = 36$  and has morphological features somewhat intermediate between the diploid species *T. rhombifolia* and *T. montana*, both with  $2n = 18$ . Perhaps the formation of amphiploids was preceded by some gene exchange between *T. rhombifolia* and *T. montana* at the diploid level. The present ranges suggest that extensive introgression between these taxa was not likely. It should prove interesting to test these various hypotheses using molecular characters. Regardless, we believe that the taxonomic community is best

served at the present time with the taxonomic treatment adopted here, this being clearly depicted to those working with living populations in the field.

Isely (1981) maps, but does not cite, at least five collections of *Thermopsis divaricarpa* (as *T. montana* var. *divaricarpa*) from western Montana, but we believe these to be misidentified elements of *T. montana* var. *montana* or *T. rhombifolia*. In addition, he maps at least a few collections of *T. divaricarpa* from northeastern Wyoming that we believe to be misidentified elements of fairly typical *T. rhombifolia*.

Isely (1981) included *Thermopsis pinetorum* as a synonym of his *T. rhombifolia* var. *montana* but examination of type material, as noted above, shows that the name apparently was typified by mixed collections; the lectotype belongs to his variety *divaricarpa*.

Nelson, in his original description of *T. divaricarpa*, provided excellent illustrations of the fruiting branches of *T. montana*, *T. divaricarpa*, and *T. rhombifolia*, along with a seemingly intermediate branch between *T. rhombifolia* and *T. divaricarpa* that he named *T. arenosa*. Although we relegate the latter name to synonymy under "typical" *T. rhombifolia*, in truth, *T. arenosa* is probably a hybrid or introgressed individual between *T. rhombifolia* and *T. divaricarpa*.

**3. *Thermopsis fraxinifolia*** (Nutt. ex Torrey & A. Gray) M. Curtis, Amer. J. Sci. 44: 81. 1843. *Baptisia fraxinifolia* Nutt. ex Torrey & A. Gray, Fl. N. Amer. 1: 387. 1840. *Thermopsis mollis* var. *fraxinifolia* (Nutt. ex Torrey & A. Gray) Isely, Brittonia 30: 469. 1978. TYPE: U.S.A. North Carolina: Burke Co., Table Mountain ("Catawba Ridge" of Nuttall; Graustein, 1967), Nuttall 1816 (holotype, PH; possible isotypes, GH, NY).

There remains a problem with the correct author citation for *Thermopsis fraxinifolia*. This is summarized by Wilbur (1963) who contended that the correct citation should be *T. fraxinifolia* M. Curtis ex A. Gray (published in 1848). Isely (1978) accepted this, but he subsequently took up the citation *T. fraxinifolia* Nutt. ex Torrey & A. Gray (1840) (Isely, 1981). We believe this to be the preferred citation because Torrey & Gray (1840) cited a Nuttall specimen and quoted a description provided by him in their discussion of *T. fraxinifolia*. Contrary to Wilbur's observation, the Nuttall name was not rejected by Torrey & Gray. They merely noted that the species had not fallen under their observation and that it was "uncertain whether it



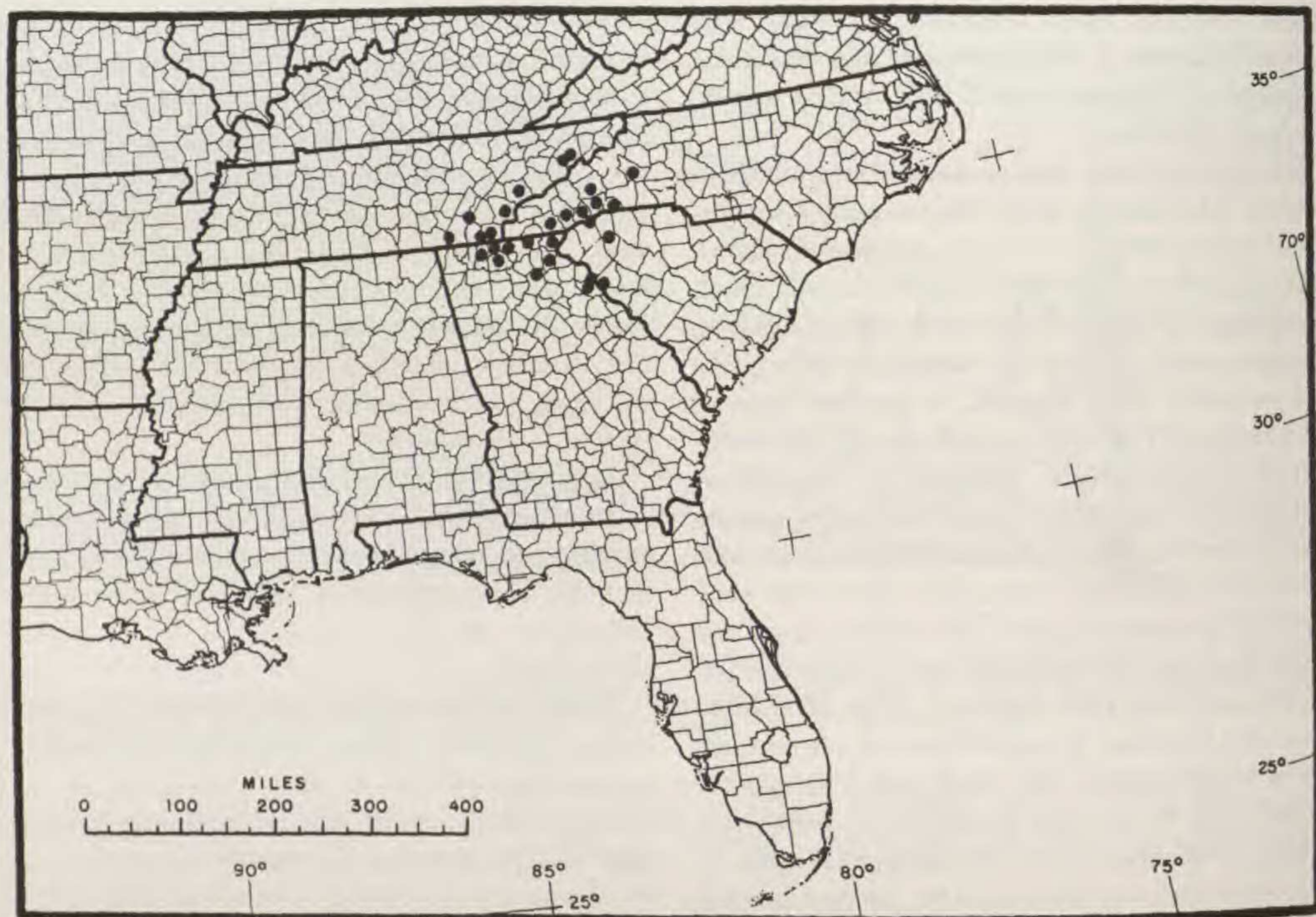


FIGURE 3. Distribution of *Thermopsis fraxinifolia*.

[*T. fraxinifolia*] be distinct from some of the species described above." We do not view this as a rejection of the name, but rather a form of abeyance.

Plants delicate, 5–10 dm tall, glabrate to sparsely puberulent; stems slender, erect, clustered, well-branched, arising from a single woody rootstock; branches spreading at 45–80°, strongly zigzagged. Leaflets elliptic, 4.5–8 cm long, 2–3.5 cm wide, acute to acuminate, glabrous to very sparsely puberulent, lateral veins 9–12 pairs, very conspicuously net-veined beneath; petioles 1.6–3 cm long; stipules sometimes persistent, lanceolate to narrowly ovate, 1–3.5 cm long, 0.3–0.8 cm wide, cuneate, acuminate. Racemes terminal or lateral, 12–25 cm long, with 7–25 flowers, scattered; peduncles 2.5–5.5 cm long; pedicels 7–17 mm long, glabrate; bracts persistent, lanceolate, 8–12 mm long, 1–3 mm wide. Flowers 1.6–1.9 cm long; calyx 7–9 mm long, 4–5 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wings elliptic to asymmetrically oblong-elliptic; keel asymmetrically oblong-elliptic; ovary appressed pubescent; ovules (6–)12–16. Pods straight, irregularly divergent, (3–)5.5–7.5 cm long, 0.3–0.5 cm wide, inconspicuously pubescent. Seeds (5–)10–15, brown, reniform with a very short rostrum, 4

mm long, 2.5 mm wide. Chromosome number,  $2n = 18$ .

*Distribution and ecology* (Fig. 3). Southernmost Appalachian Mountains in eastern Tennessee, western North Carolina and adjacent Georgia and South Carolina, rich woods, mostly upper hillslopes along streams and at lower elevations along floodplains, (300–)700–1600 m; flowering (April–)May–July.

*Representative specimens examined.* U.S.A. **Georgia:** Fannin Co., NE of Cisco and NW of Blue Ridge, along Jack's Trail and Jack's River, 6 June 1983, *Coile et al.* 3610 (RM, TENN). Gilmer Co., near Stanley Gap, 7 June 1982, *Coile et al.* 2844 (POM, TEX). Habersham Co., *Small* 1895 (ARIZ, F, NY). Hall Co., near Gainesville, *Huger* 1897 (NY). Murray Co., mountain slopes between Cohutta and Fort Mountains, 27 May 1935, *Duncan & Hardin* 16468 (NCU). Oglethorpe Co., ca. 0.75 mi. S of the Georgia Hwy. 368 bridge over the Savannah River, 200 m, 7 June 1979, *Credle* 863 (NCU); near bridge of Georgia Hwy. 72 on Savannah River, 10 June 1978, *Robert & Coile* 1860 (NCU). Rabun Co., Rabun Bald, 1–4 June 1906, *House* 2266 (US); Tallulah Falls, *Small* 1893 (F, NY). Towns Co., Young Harris, 10 July 1908, *Howell* 390 (MO, US). **North Carolina:** Buncombe Co., Black Mountain, 12 Aug. 1905, *Biltmore Herbarium* 11214 (F, GH, MO, NY, US); Asheville, *Kraus* 1925 (MO, POM, UC). Burke Co., vicinity of Table Rock Mt., 2 Aug. 1890, *Heller* 27 (F, MO, NY, POM, UC). Henderson Co., Flat Rock, *Gibbes* 1854 &



1858 (NY). Macon Co., 1.4 mi. N of the Georgia state line on North Carolina Route 28, 1 June 1975, *Wood & Boufford 1389* (A); 2.1 mi. N of the Georgia state line on North Carolina Route 28, 1 June 1975, *Boufford 16075* (MO). Polk Co., Pony Mt., *Townsend 1897* (US). Transylvania Co., Whitewater River, just above Upper Falls, 7 June 1951, *Godfrey 51298* (MO). Yancey Co., Mt. Mitchell, *Rhoades 1932* (GH, PH, RM); E of Mt. Mitchell, exactly 2.3 mi. SW of Rough Ridge Tunnel, 30 June 1970, *Turner 6076* (ARIZ, CAS, F, MO, NY, TEX). **South Carolina:** Abbeville Co., 3 mi. SW of Calhoun Falls, near Savannah River, 13 May 1957, *Radford 22768* (NCU, UC). Greenville Co., Caesars Head, *Smith 1881* (F, GH, MO, NY, US). Oconee Co., *Boynton 1889* (CAS). Pickens Co., 0.7 mi. off U.S. Hwy. 178 on Sassafras Mt. Road, 30 June 1970, *Turner 6075* (ARIZ, CAS, COLO, F, GH, MO, NCU, NY, RM, TEX, WTU). **Tennessee:** Blount Co., Chilhowee Mountain, 10.98 km SW of Tennessee Hwy. 73 on Foothills Parkway, 650 m, 26 May 1982, *Boufford & Spongberg 22881* (A, MO, NCU, POM, TEX). Greene Co., 2.3 road mi. S of Camp Creek School, just N of Horsehitch Gap, 10 June 1980, *Boom & Smith 547* (TENN); along Kennedy Cabin loop road, 11 June 1980, *Boom & Perkins 554* (TENN); mountain slope between Camp Creek and Paint Creek on Green Mt., 30 July 1950, *Shanks & Sharp 7455* (TENN). Hamilton Co., Lookout Mt., *Canby 1869* (F, GH, MO, NCU, NY, PH, US). Monroe Co., Waucheesi Mt. on FR 126-C, 12 June 1978, *Whitten & Mescall 213* (TENN). Polk Co., Peavine Road, 5.8 road mi. SW of Ocoee No. 3 Powerhouse, 23 May 1980, *Boom 471* (TENN); Wolf Ridge, 25 June 1983, *Z. E. & J. B. Murrell 336* (TENN). **Cultivated:** Massachusetts, Botanical Garden of Cambridge, *Gray s.n.* (NY).

This species is partially sympatric with *Thermopsis mollis*, but in regions of overlap *T. fraxinifolia* usually occurs at higher elevations along the upper slopes of the mountainous ridges and hills of the Appalachians. *Thermopsis fraxinifolia* may also occur at lower elevations on alluvial deposits along at least some of the rivers in this region.

*Thermopsis fraxinifolia* can be distinguished from *T. mollis* by its more robust, more branching habit, lateral (as well as terminal) inflorescences, and longer pedicels. Furthermore, *Thermopsis mollis* propagates by extensive, vigorous rhizomes, which are absent in *T. fraxinifolia*. Both species were well known to Asa Gray, who personally collected *T. fraxinifolia* at its type locality and subsequently grew this at the botanical gardens at Harvard. According to Gray (1848b), *T. mollis* was also maintained in the Harvard Botanical Gardens at the same time. Living specimens of both were used to make the excellent illustrations of the two species that accompany his treatment of *Thermopsis* of the eastern United States.

As noted by Gray (1848b), Wilbur (1963), and Radford et al. (1968), *Thermopsis mollis* is mostly a piedmont species, distributed along the middle and western portions of North Carolina and adja-

cent states, occasionally extending into the mountains, where its range abuts that of *T. fraxinifolia*. Indeed, we do not know of any specific sites where the two have been collected together, nor do we perceive a large set of intermediate plants in regions of near contact (or elsewhere) that might justify their recognition as regional variants of a single species, as treated by Isely (1981). His distribution maps of both taxa are fairly accurate, although these are difficult to evaluate since he did not cite specimens documenting the distributions shown.

Isely (1981) did map a number of specimens from easternmost Tennessee that appear to be anomalous. These are morphologically somewhere between *Thermopsis mollis* and *T. fraxinifolia* and were designated "*T. mollis* var.?" on Isely's map. We believe that many of these may be derivatives of hybridization between *T. mollis* and *T. fraxinifolia*. The species occur in close proximity in this region and the intermediates have the habit of *T. mollis* but the inflorescence pattern and general habitat preference of *T. fraxinifolia*. Both *T. mollis* and *T. fraxinifolia* have been collected on Lookout Mountain, Hamilton Co., Tennessee, as have several of the putative hybrid intermediates (e.g., *Churchill 1911*, TENN; *Canby 1869*, GH, MO, NCU, NY, PH, US).

More detailed field investigations may show that the hypothetical hybrids may, in fact, be part of a more widespread, highly variable taxon derived from ancestral hybridization between *Thermopsis mollis* and *T. fraxinifolia*. This is inferred from recent collections by Boufford & Spongberg from Blount Co., Tennessee (22881, GH, MO, NCU, TEX), and by Whitten from Monroe Co., Tennessee (213, TENN), which seem to reveal stabilized populations of intermediate morphology in this area. Some of the characters in at least a few of these plants are unique within the American taxa of *Thermopsis*. For example, the Blount County specimens cited above have short, squat pods with distinct gynophores, much as occurs in some of the Asian species. On the present information, however, it is more sensible to include such plants within a variable *T. fraxinifolia* than to accord these varietal status.

4. ***Thermopsis gracilis*** Howell, *Erythea* 1: 109. 1893. TYPE: U.S.A. Oregon: Josephine Co., "Mountains near Waldo," 5 July 1887, *T. J. Howell 669* (holotype, ORE; isotypes, CAS, GH).

*Thermopsis venosa* Eastw., *Bull. Torrey Bot. Club* 32: 198. 1905. *Thermopsis gracilis* var. *venosa* (Eastw.) Jepson, *Man. Fl. Pl. Calif.* 515. 1925. *Thermopsis*



*montana* var. *venosa* (Eastw.) Jepson, Fl. Calif. 2: 245. 1936. *Thermopsis macrophylla* var. *venosa* (Eastw.) Isely, Brittonia 30: 469. 1978. TYPE: U.S.A. California: Shasta (or Trinity) Co., "Lewiston Trail near the summit that divides Trinity from Shasta County, California," Eastwood 1901 (holotype, CAS).

*Thermopsis subglabra* L. Henderson, Rhodora 32: 26. 1930. TYPE: U.S.A. Oregon: Lane Co., "Shady woods of Culp Creek, near base of Bohemia Mt. Divide, between Lane and Douglas Counties, Oregon," 1600 m, 2 May 1926, J. R. Patterson 9959 (lectotype, selected here, ORE).

In his protologue for *Thermopsis gracilis*, Howell did not mention a specific type but rather noted the species to occur in "Mountains of southwestern Oregon, from the sources of the Willamette, to northern California," which suggests that he knew the plant from a number of collections. Actually, there is only a single sheet at ORE that could have served as the voucher for *Thermopsis gracilis*. L. A. Vorobik, by annotation, selected this as the holotype. A purist might have called this a lectotype.

Plants robust, 3–8 dm tall, glabrous to sparsely villous; stems slender, erect, single or clustered, well-branched, arising from a woody rootstock or rhizomes, branches spreading at 30–70°, moderately to strongly zigzagged. Leaflets elliptic to obovate or rhombic, 3–6(–8) cm long, 2–3.2 cm wide, acute, obtuse, or emarginate, glabrous, lateral veins 6–9 pairs, very conspicuously net-veined beneath; petioles 2.5–4(–5) cm long; stipules persistent, asymmetrically ovate-elliptic, 2.5–3.5 cm long, 1.5–3 cm wide, cuneate to cordate, acuminate. Racemes 12–20(–30) cm long, with 7–30 flowers, scattered; peduncles 4–9(–11) cm long; pedicels 6–16 mm long, glabrous to sparsely villous; bracts semipersistent, ovate, 6–8 mm long, 3–5 mm wide. Flowers 2–2.3 cm long; calyx 8–10 mm long, 7–8 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wings elliptic; keel asymmetrically oblong-elliptic; ovary sparsely villous; ovules 9–14. Pods straight, irregularly divergent, 3–6 cm long, 0.4–0.6 cm wide, inconspicuously pubescent. Seeds 2–8, tan, oblong with a short rostrum, 3–4 mm long, 2 mm wide. Chromosome number,  $2n = 36$ .

**Distribution and ecology** (Figs. 1, 4). Northwestern California and adjacent Oregon, mesophytic lower montane evergreen forests, mostly 100–1200 m; flowering (April–)May–June.

**Representative specimens examined.** U.S.A. California: Del Norte Co., Siskiyou lowlands near Gasquet, 22 Apr. 1939, Meola 69 (OSC, UC); N side of Middle Fork of Smith River on Old Gasquet Toll Road, 1 June

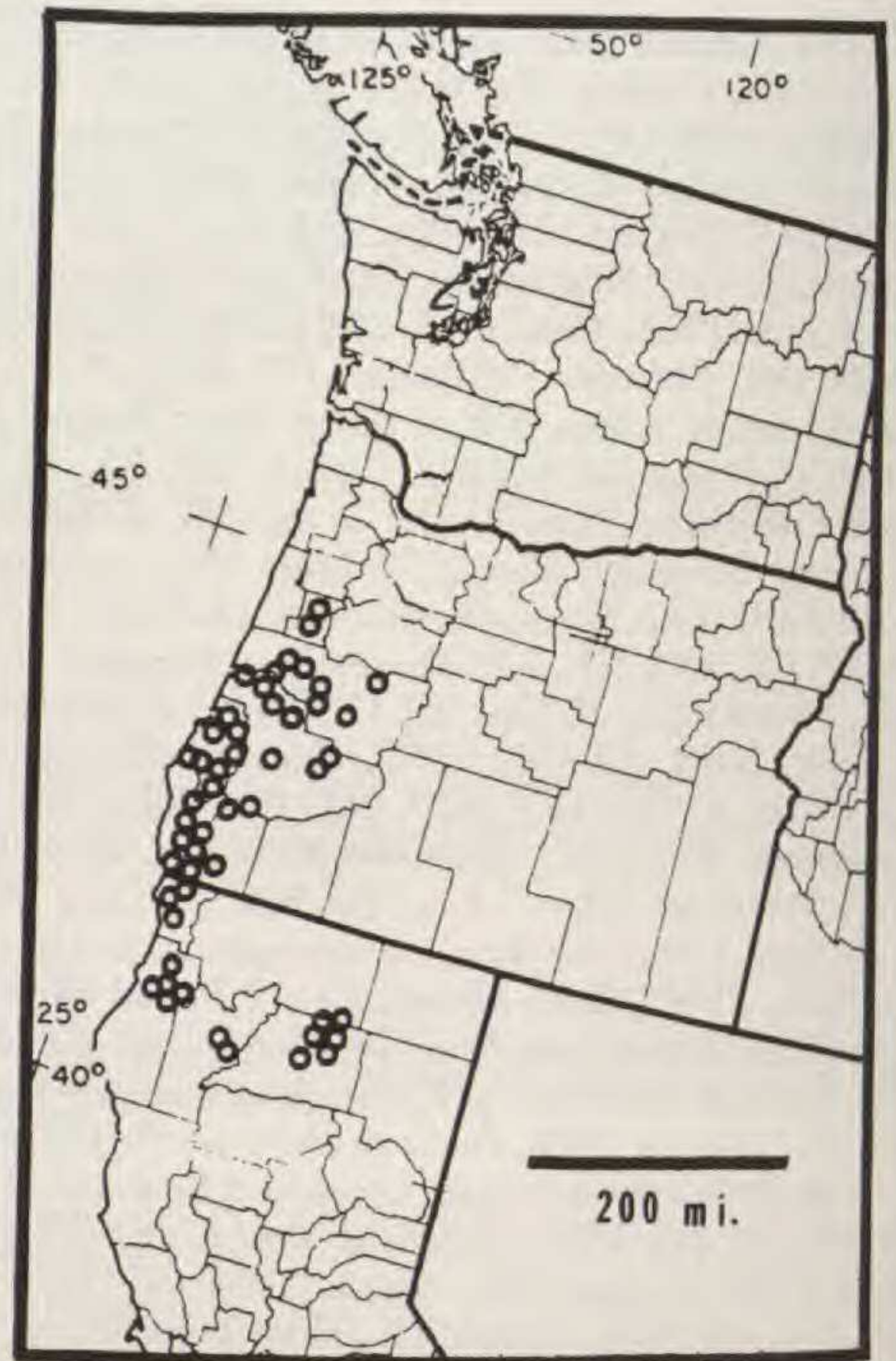


FIGURE 4. Distribution of *Thermopsis gracilis*.

1935, Parks & Tracy 11227 (CAS, GH, UC, WTU); 2 mi. S of Gasquet on French Hill Road, 1 June 1968, Turner 5801 (CAS, GH, NY, TEX). Humboldt Co., French Camp Ridge, in chaparral, 6 Aug. 1933, Tracy 12955 (UC, WTU); Willow Creek Canyon, along Trinity Hwy., rocky point at Ruby Creek, 31 May 1937, Tracy 15326 (UC, WTU). Shasta Co., between La Moine and Williams Ranch, 19 June 1919, Heller 13250 (CAS, GH, MO, NY, PH, UC, WTU); McCloud Fork, 24 Apr. 1913, Smith 110 (GH, MO, NY). Siskiyou Co., Dunsmuir, 23 July 1912, Eastwood 1319 (CAS, GH, MO, NY, US); ca. 2 mi. S of Shasta Springs, on the old McCloud Road, 2 June 1968, Turner 5807 (TEX). Trinity Co., E of Weaver Creek, 21 May 1914, Yates 7-72 (RM, US). Oregon: Benton Co., Mary's Peak Road, ca. 10 mi. SW of Corvallis, Mills 1973 (UT); Philomath, 23 May 1925, Stason 2399 (UC). Coos Co., 3 km NE of Remote, 7 May 1980, Sundberg 994 (OSC). Curry Co., 2 mi. SW of turn-off from road to Agness along road to Iron Mt., 16 June 1956, Balls & Lenz 21697 (CAS, NY, POM, RM, UC, UT, WS); Mt. Emily, lower chaparral belt, 10 Aug. 1921, Jepson & Tracy 5909 (TEX, UC). Douglas Co., Dog Creek drainage of N. Umpqua River upstream from Steamboat River, above Limpy Rock, 19 June 1976, Chambers 4223 (CAS, NCU, POM, WTU); 10 mi. from West Fork, 27 June 1917, Peck 7255 (F, OSC). Jackson Co., Grave Creek near Winarr, 14 May 1889, Hammond 74 (MO). Josephine Co., summit of the lower Siskiyou Mts. especially N slopes, 3 July 1902, Cusick 2927 (F, GH, MO, NY, OSC, POM, UC, US, WS); Waldo, July 1894, Howell 1495 (COLO, MO, NY, ORE, OSC, PH, UC, US, WS, WTU); Onion Mt. Road, 11 May 1956, Steward 7059 (CAS, MO, NCU, OSC, PH, POM, TENN); Sexton Mt., 9 Apr. 1934, Thompson 10209 (CAS, NY, POM, WYU). Lane Co., Spencer's Butte, 4 mi. S of



Eugene, 5 May 1946, *Baker 2791* (ARIZ, CAS, MO, NY, OSC, WTU); near Cottage Grove, Lorane Road, 17 May 1931, *Henderson 13574* (PH). Lincoln Co., Alsea Mts., *Lammi 1939* (OSC). Polk Co., 2 mi. W of Grand Ronde, *Brehm 1967* (TEX).

This species is readily distinguished from the closely allopatric *Thermopsis californica* and *T. montana* by its divergent pods, spreading branches, and glabrous to sparsely pubescent foliage. It is most closely related to *T. robusta*, which also has divergent pods but which differs in its very robust habit, densely pilose vestiture, and longer calyx lobes. Larisey (1940) maintained *Thermopsis venosa* as a variety of *T. gracilis*, but Isely (1981) treated both names as synonyms under *T. macrophylla* var. *venosa*. If Isely's treatment is accepted, the correct taxon name under the existing nomenclatural code would be *Thermopsis macrophylla* var. *gracilis*, since that combination was validated with the erection of *T. gracilis* var. *venosa*. Regardless, we feel that *T. gracilis* is clearly distinct from *T. macrophylla*, as discussed in detail under the latter.

5. ***Thermopsis macrophylla*** Hook. & Arn., Bot. Beechey Voy. 329. 1840. TYPE: U.S.A. California: Santa Barbara Co.?, spring of 1833?, probably Santa Ynez Mt., near Santa Barbara, *Douglas s.n.* (holotype, K; photo of holotype, POM, UC; isotype, GH).

*Thermopsis macrophylla* var. *agnina* J. Howell, Leaflet W. Bot. 8: 158. 1957. TYPE: U.S.A. California: Santa Barbara Co., Camino Cielo, ca. 1 mi. W of Santa Ynez Peak, ca. 1060 m, *H. M. Pollard 1955*, plant B, 2 sheets (lectotype, selected here, CAS; isolectotypes, CAS [2 sheets plant A], US [3 sheets]).

Many workers have pondered over the type locality of *Thermopsis macrophylla*, equating *Thermopsis macrophylla* with *Thermopsis californica* S. Watson, but examination of type material and knowledge of the variation of *Thermopsis californica* throughout its range strongly suggest that *Thermopsis macrophylla* was originally collected in the Santa Ynez Mountains near Santa Barbara. Douglas resided for a time in Monterey, Santa Cruz County, California, from where he made several overland visits to Santa Barbara Mission. Eastwood, as noted by Howell (1957), thought she might have rediscovered the type locality of *Thermopsis macrophylla* in the Santa Cruz Mountains, Santa Cruz County, California, near Glenwood, but examination of this material (*Davis 1907*, CAS, GH, RM, UC, US) reveals these to be robust forms of otherwise typical *Thermopsis californica*. Howell also discussed the possible type locality of *Ther-*

*mopsis macrophylla* in connection with his description of *T. macrophylla* var. *agnina*, suggesting a type locality for *T. macrophylla* near Aromas in San Benito County. But these, too, are merely large-leaved forms of otherwise typical *Thermopsis californica*. Type specimens of *Thermopsis macrophylla* match very closely those of *T. macrophylla* var. *agnina* and had Howell examined material of the Douglas collection we believe he would not have described the latter. No doubt much of the confusion regarding recognition of both *Thermopsis macrophylla* and *T. californica* is due to the fact that *T. macrophylla* is a relatively rare localized endemic. This has been confounded by the existence of *Thermopsis robusta*, a localized robust endemic with divergent pods, which is related to *T. gracilis* but is superficially similar to *T. macrophylla* in habit and vestiture. At least several workers who have recognized *Thermopsis macrophylla* as distinct from *T. californica* have treated both *T. macrophylla* and *T. robusta* as the same.

Plants robust, 12–23 dm tall, tomentose; stems thick, erect, solitary or few, moderately branched, from a woody rootstock, branches ascending at 45°, moderately zigzagged. Leaflets elliptic, 4–10 cm long, 2–5 cm wide, villous, acute, lateral veins 6–8 pairs, not conspicuously net-veined beneath; petioles 2–5(–7) cm long; stipules persistent, widely ovate, 3–9 cm long, 2–6 cm wide, amplexicaul to cordate, acuminate. Racemes 25–60 cm long, with 30–90 flowers, in whorls of 3–5; peduncles 8–15 cm long; pedicels 2.5–4 mm long, villous; bracts persistent, ovate to lanceolate, 8–10 mm long, 3–5 mm wide. Flowers 1.7–2.2 cm long; calyx 7–9 mm long, 7–8 mm wide at the limb, lobes 3–4 mm long, as long as or shorter than tube; wings elliptic; keel obovate; ovary velutinous; ovules 7–9. Pods straight, ascending, 3.5–5 cm long, 0.5–0.7 cm wide, villous. Seeds 5–7, brown-black, widely elliptic with a short rostrum, 4–5 mm long, 2.5–3.0 mm wide. Chromosome number,  $2n = 18$ .

*Distribution and ecology* (Fig. 1). Known only from the Santa Ynez Mountains, Santa Barbara Co., California, where it is locally common on the west side of Santa Ynez Peak near the summit, in sandy granitic soils, 1000–1400 m; flowering May–June.

*Specimens examined*. U.S.A. **California**: Los Angeles Co., Claremont, weed on the Rancho Santa Ana Botanic Garden grounds, “apparently introduced,” 9 May 1991, *Ross 5047* (POM). Santa Barbara Co., S slope of Santa Ynez Peak, 1130 m, 11 May 1962, *Breedlove 2695* (CAS, POM); Santa Ynez Peak, *Fairfax 1977* (RM); Santa Ynez Peak, ca. 4000 ft., *Pollard 1956* (CAS,



TEX); in chaparral W of Santa Ynez Peak, 17 Oct. 1945, *Smith 1620* (POM); just W of Santa Ynez Peak, 12 May 1957, *Smith 5283* (POM); ca. 0.5 mi. due W of Santa Ynez Peak, 4 June 1968, *Turner 5820* (GH, NY, TEX); Santa Ynez Mts., along W Camino Cielo Road, 5.5 mi. E of intersection with Refugio Road, 3900 ft., 26 June 1992, *Junak 5022* (TEX); Santa Ynez Mts., along W Camino Cielo Road, 6.2 mi. E of intersection with Refugio Road, 4020 ft., 26 June 1992, *Junak 5020* (TEX).

The relationship of this localized endemic and its longtime confusion with *Thermopsis californica* is discussed in the above account of its typification. The early workers, mainly S. Watson, who possessed an isotype of *T. macrophylla*, maintained both *T. californica* and *T. macrophylla* as conceived in the present study. Subsequent workers, mostly Californian, confounded the two taxa. The taxa were not clarified by Larisey (1940), who treated both *T. californica* and *T. robusta* as synonymous with her *T. macrophylla* var. *macrophylla* (she ignored *T. macrophylla* var. *agnina*). In this Larisey was followed by Isely (1981) who also treated all of these as synonymous with his concept of *T. macrophylla* var. *macrophylla*. To our knowledge, Douglas made only two collections of *Thermopsis* in California, the type of *T. macrophylla* and a collection of *T. californica* var. *californica*. Torrey & Gray (1840) referred the latter to *T. macrophylla* var.  $\beta$ . This specimen (GH) is a fairly typical specimen of *T. californica*, presumably collected in the spring of 1833, perhaps in the vicinity of Monterey, California, to judge from its flowering state and vestiture.

- 6. *Thermopsis mollis*** (Michaux) M. Curtis ex A. Gray, Mem. Amer. Acad. Arts n.s. 3: 47. 1848. *Podalyria mollis* Michaux, Fl. Bor.-Amer. 1: 264. 1803. *Baptisia mollis* (Michaux) Nutt., Gen. N. Amer. Pl. 1: 281. 1818. TYPE: U.S.A. North Carolina: Mecklenburg Co., vicinity of Mecklenburg, without date, *Michaux s.n.* (holotype, P not seen; probable isotype, PH).

*Baptisia hugeri* Small, Bull. Torrey Bot. Club 25: 139. 1898. *Thermopsis hugeri* (Small) Small, Fl. S.E. U.S. 596, 1331. 1903. TYPE: U.S.A. Georgia: Habersham Co., "northern slope on Mount Griffin," near Cornelia, *A. M. Huger* 1897 (holotype, NY; isotype, MO).

Plants delicate, 3–6 dm tall, sparsely appressed pubescent; stems slender, ascending or spreading, solitary or clustered, moderately branched, arising from extensive rhizomes; branches spreading at 45–80°, strongly zigzagged. Leaflets elliptic, 3.5–8 cm long, 1–4 cm wide, acute to acuminate, sparsely appressed pubescent especially on veins,

sometimes glabrate above, lateral veins 7–9 pairs, very conspicuously net-veined beneath; petioles 0.7–1.7 cm long; stipules caducous, narrowly elliptic to linear, 1.5–2 cm long, 0.3–0.5(–0.8) cm wide, cuneate, acuminate. Racemes terminal, 7–20 cm long, with 5–17 flowers, scattered; peduncles 3–7 cm long; pedicels 4–6 mm long, villosulous; bracts persistent, lanceolate, 8–13 mm long, 2–4 mm wide. Flowers 1.6–1.9 cm long; calyx 7.5–8 mm long, 6–7 mm wide at the limb, lobes 2–3 mm long, shorter than tube; wings elliptic to asymmetrically oblong-elliptic; keel asymmetrically oblong-elliptic; ovary densely appressed pubescent; ovules (8–)12–16. Pods arcuate to straight, divergent, (3–)4–9 cm long, 0.4–0.6 cm wide, densely appressed pubescent. Seeds 6–12, oblong with a rostrum, 2.5–3.5 mm long, 1.5–2 mm wide. Chromosome number,  $2n = 18$ .

*Distribution and ecology* (Fig. 5). Mostly mid-elevations of the southern Appalachian Mountains and adjacent piedmont region of northernmost Georgia, eastern Tennessee, northwestern South Carolina, western North Carolina, and central Virginia, mostly 300–800 m; flowering (April–)May–June.

*Representative specimens examined*. U.S.A. **Alabama**: De Kalb Co., Mentone, *Loving* 1899 (US). **Georgia**: Dade Co., 1 mi. W of Durham and NE of Cloudland Canyon, 12 May 1953, *Hardin 15933* (NCU, US); Look-out Mt., 26 Apr. 1952, *Harper 4204* (NY, US). Habersham Co., near Cornelia, *Huger* 1898 (NY). Walker Co., 22.4 mi. SE of La Fayette, 24 Apr. 1961, *Turner 4691* (TEX). Whitfield Co., 4 mi. NW of Dalton, 24 Apr. 1948, *Cronquist 5055* (NY); near summit of Chattoogata Mts., 19 July 1990, *Harper 265* (NY, US). **North Carolina**: Buncombe Co., [Asheville], Biltmore, 1 May–10 June 1896, *Biltmore 1025* (F, MO, NY, PH, RM, TENN, UC, US). Caswell Co., Milton, *Fomey* 1860 (PH). Catawba Co., 3 mi. SSE of Newton, 29 Apr. 1957, *Bell 6822* (NC, NY); 1.25 mi. SW of Hickory on U.S. Hwy. 70, 3 May 1953, *Radford & Wood 6970* (NCU, US). Chatham Co., vicinity of Bush Creek, 3.9 mi. S of Orange Co. line on U.S. Hwy. 15 and 0.6 mi. E on paved road, 24 Apr. 1957, *Ahles 23825* (GH, NCU); Edward's Mt., 3 mi. E of U.S. Hwy. 501, 6.6 mi. S of Chapel Hill, 11 Apr. 1940, *Radford & Steward 77* (NCU). Durham Co., Lynn 1933 (ND). Forsyth Co., *Schallert* 1940 (GH); S edge of Winston-Salem, *Wherry* 1928 (NY). Gaston Co., near summit of Kings Mt., 24 Apr. 1968, *Leonard & Radford 1353* (LL, NCU, OSC, TENN, TEX); Crowders Mt., 4 June 1953, *Radford & Haesloop 7089* (ARIZ, NCU). Guilford Co., Guilford College, 30 Apr. 1958, *Terrell 3205* (NCU). Henderson Co., Flat Rock, *Memminger* 1886 (NCU). Iredell Co., 3.3 mi. W of Harmony on North Carolina Hwy. 901, 21 Apr. 1953, *Daggy 2221* (NCU); Statesville, *Hyams 4968* (F, MO, NY, POM). Lincoln Co., *Hunter s.n.* (GH, NY); near Vale, 28 Apr. 1957, *Bell 6654* (NCU). Orange Co., near Hillsboro, *Curtis s.n.* (NY). Stokes Co., 1 mi. N of Hanging Rock, 30 Apr. 1961, *Carswell 192* (NCU); above Danbury, *Hunt* 1936 (NCU). Surry Co., Pilot Mt., *Ashe* 1896



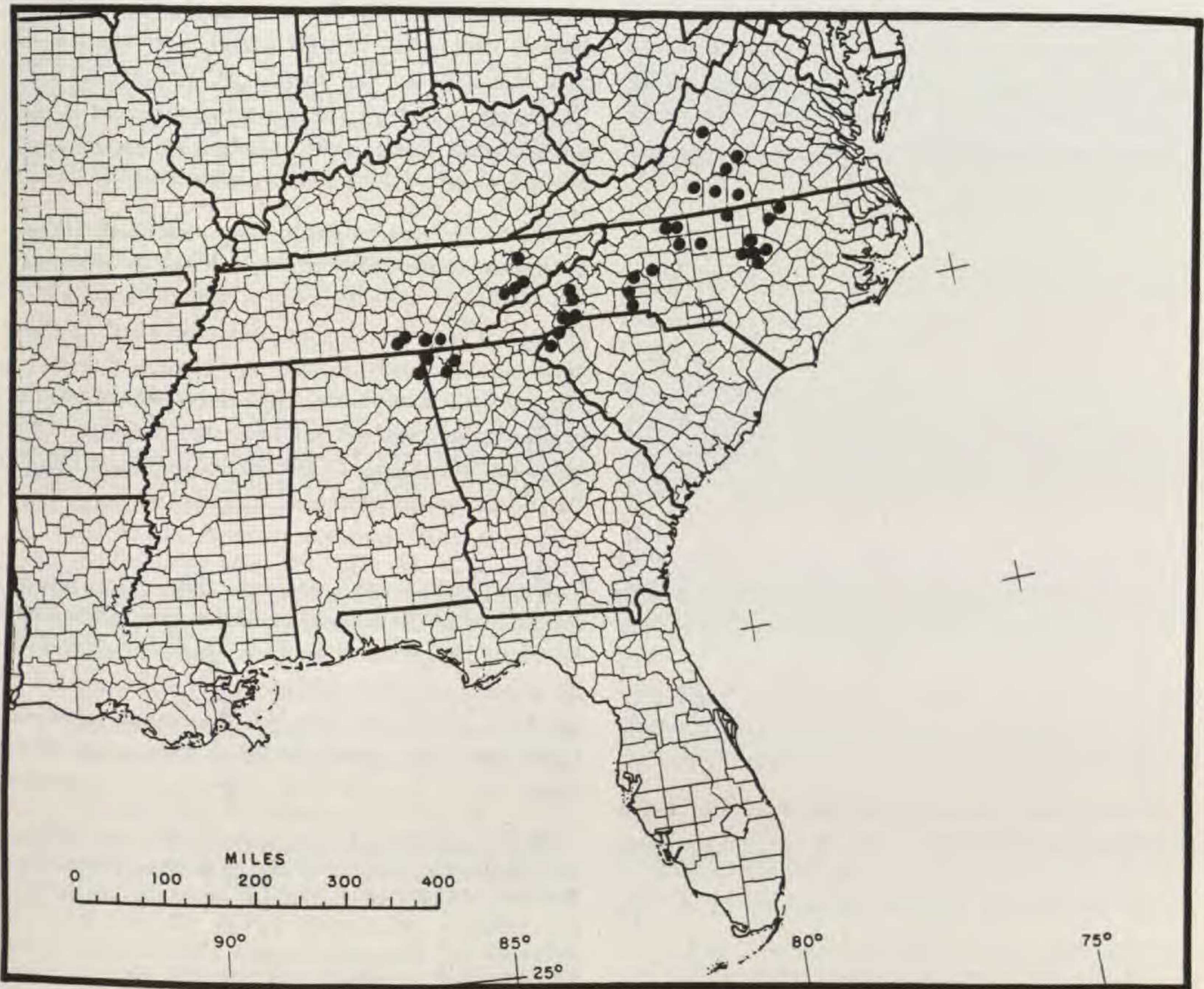


FIGURE 5. Distribution of *Thermopsis mollis*.

(NCU); Pilot Mt., 5 May 1935, *Oosting* 3519 (NCU). Vance Co., Kittrell, *Browne* 1884 (NY); Kittrell's Springs, *Faxon* 1874 (GH). Wake Co., 5.5 mi. NE of Holly Springs, 28 Apr. 1954, *Radford & Beard* 7984 (NCU); W of Raleigh, 1 mi. N of Tyson's Store, 30 Apr. 1951, *Fox* 4580 (MO). Warren Co., Ridgeway, 20 Apr. 1938, *Godfrey* 3600 (GH, NCU). **South Carolina:** Greenville Co., Paris Mt., *Huger* 1903 (NY); Paris Mt., *Huger* 1904 (NY). Oconee Co., Rich Mt., 5.5 mi. W of Walhalla, 16 Apr. 1967, *Bozeman et al.* 8862 (COLO, NCU, POM, WTU); Mountain Rest, ca. 0.5 mi. W of West Village Creek on County Route 258, 30 Apr. 1989, *Hill* 20511 (NY). Pickens Co., 12.5 mi. S of Rosman along U.S. Hwy. 178, 1 May 1941, *McVaugh* 5649 (GH, UC). **Tennessee:** Blount Co., Chilhowee Mt., 26 Apr. 1939, *Jennison* 299 (TENN); Chilhowee Mt., between Millstone Gap and Walland, *Thomas* 1965 (TENN). Franklin Co., edge of Sewanee, 3 May 1941, *Sharp & Meyer* 1259 (MO, PH, TENN, UC); St. Andrews, 25 Apr. 1936, *Svenson* 7592 (GH, MO, PH, UC). Grainger Co., Lea Lakes, 3 May 1934, *Hesler & Sharp* 566 (TENN). Hamilton Co., Lookout Mt., *Churchill* 1906 (GH); Lookout Mt., *Churchill* 1906 (GH, MO, TENN). Marion Co., W of Whitwell, 14 May 1934, *Harger* 7788 (GH, TENN). Sevier Co., Gatlinburg entrance to Great Smoky Mountains National Park, *Rogers* 41851 (TENN); Chilhowee Mt., 7 May 1964, *Thomas* 32794 (TENN). **Virginia:** Bedford Co., intersection of County Route 711 and County Route 811, 11 Aug. 1985, *Wright* 469 (MO). Camp-

bell Co., Sleepy Hollow Road, 23 May 1967, *Freer* 5597 (GH, NCU). Charlotte Co., 4 mi. S of Charlotte, Court House township, 16 Apr. 1967, *Harvill* 15436 (NCU). Halifax Co., near Halifax, *Rowlett* 1921 (US). Prince Edward Co., Hampden Sydney College, *Blair* 1981 (F, GH, MO, NY, US); Farmville, *Fattig* 1922 (US). Rockbridge Co., Balcony Falls, 1 May 1947, *Freer* 1348 (GH).

The relationship of this species to *Thermopsis fraxinifolia* is discussed under *T. fraxinifolia*.

Fernald (1950) noted that at least one population of *Thermopsis mollis* from Essex Co., Massachusetts, had been introduced and naturalized in the northeastern United States, although he ignored the more widely cultivated *T. villosa*. We have examined material from Essex Co. (GH), presumably that referred to by Fernald, but it appears to be *T. villosa*.

**7. *Thermopsis montana* Nutt. ex Torrey & A. Gray, Fl. N. Amer. 1: 388. 1840. TYPE: see *Thermopsis montana* var. *montana*.**

Plants delicate, 2-8(-10) dm tall, glabrous to appressed pubescent or thinly villous; stems slender, erect, solitary or clustered, moderately or few-



branched, arising from a woody rootstock or rhizomes; branches ascending at 20–45°, weakly to moderately zigzagged. Leaflets narrowly elliptic or obovate, 3.5–8 cm long, 0.7–3(–5) cm wide, acute or obtuse, sometimes short mucronate or emarginate, sparsely appressed pubescent to glabrous, lateral veins 6–11 pairs, conspicuously net-veined beneath or not; petioles 1–4 cm long; stipules persistent, widely ovate or elliptic, 1.7–4.5 cm long, 0.7–2.5 cm wide, oblique to cuneate, acuminate or acute. Racemes 4–25 cm long, with 6–25 flowers, in whorls of 2–3 or scattered; peduncles 2–8 cm long; pedicels 3.5–5 mm long, villosulous; bracts semipersistent, narrowly elliptic to widely ovate, 6–10 mm long, 2.5–6 mm wide. Flowers 1.6–2.2 cm long; calyx 9–11 mm long, 5–8 mm wide at the limb, lobes 3–5 mm long, shorter than tube; wing and keel petals asymmetrically oblong-elliptic; ovary velutinous or densely appressed pubescent; ovules 10–16. Pods straight, erect, 4.5–6.5 cm long, 0.4–0.6 cm wide, villosulous or appressed pubescent. Seeds 6–16, brown-black, oblong with a rostrum, 3.5–5 mm long, 2.5–3 mm wide.

We recognize two intergrading varieties under this taxon, as follows:

#### KEY TO VARIETIES OF *THERMOPSIS MONTANA*

- 1a. Plants less than 7 dm tall, pubescent; stems often solitary and few-branched, often arising from rhizomes; leaflets not conspicuously net-veined beneath; bracts elliptic to widely ovate ..... 7a. *Thermopsis montana* var. *montana*
- 1b. Plants up to 10 dm tall, glabrate; stems clustered and moderately branched, arising from a woody rootstock; leaflets conspicuously net-veined beneath; bracts narrowly elliptic ..... 7b. *Thermopsis montana* var. *ovata*

**7a. *Thermopsis montana* var. *montana*.** *Thermopsis fabacea* var. *montana* (Nutt. ex Torrey & A. Gray) A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863: 60. 1864. *Thermopsis rhombifolia* var. *montana* (Nutt. ex Torrey & A. Gray) Isely, Brittonia 30: 470. 1978. TYPE: U.S.A. Wyoming: "Rocky Mountains" [Sweetwater Co.?], Nuttall 1834 (holotype, BM not seen; photo of holotype, POM, UK; isotype, PH; photo of isotype, POM).

*Thermopsis angustata* E. Greene, Pl. Baker. 3: 34. 1901. TYPE: U.S.A. Nevada: Elko Co., Star Valley, "foothills of the Ruby Mountains," E. L. Greene 1896 (holotype, ND).

*Thermopsis stricta* E. Greene, Pl. Baker. 3: 34. 1901. TYPE: U.S.A. Colorado: Gunnison Co., Gunnison, 24 July 1901, 2330 m, C. F. Baker 604 (lectotype, selected here, ND; isolectotypes, GH [2 sheets], NY RM [2 sheets], UC, US [2 sheets]).

According to the known distribution of *Thermopsis montana*, Nuttall would most likely have first encountered the species in Sweetwater Co., Wyoming, at about the time indicated. It is also possible that it was first collected in southeastern Idaho in early July (cf. Graustein, 1967).

Plants 2–7 dm tall, appressed pubescent to thinly villous; stems stiffly erect, solitary or clustered, few-branched, arising from a woody rootstock or rhizomes; branches moderately zigzagged. Leaflets elliptic to narrowly elliptic or obovate, 3.5–8 cm long, 0.7–2.5 cm wide, appressed pubescent, not conspicuously net-veined beneath; petioles 1–2.5 cm long. Racemes 4–18 cm long; bracts elliptic to widely ovate. Flowers 1.6–2 cm long. Pods villosulous. Chromosome number,  $2n = 18$ .

*Distribution and ecology* (Fig. 6). Widely distributed in the intermountain region of the United States, from southwestern Montana southward to Arizona and New Mexico and northwestward to southern Idaho and adjacent Wyoming, middle to high elevations, 2000–3200 m; flowering May–June.

*Representative specimens examined.* U.S.A. **Arizona:** Apache Co., 1 mi. N of Alpine, 27 June 1944, Pultz & Phillips 1030 (ARIZ, NY, UC). Cochise Co., Barefoot Park, Blumer 1907 (ARIZ, F, GH, MO, NY, RM, US). Coconino Co., Flagstaff, 21 Apr. 1925, Nelson 10200 (GH, MO, NY, PH, POM, RM, UC, WS). Gila Co., Sierra Ancha, Aztec Peak, 1 May 1931, Harrison 7857 (ARIZ, US). Graham Co., Graham Mts., Pine Crest, 26 May 1935, Maguire 12013 (NY, WS, WTU). Greenlee Co., near Rose Peak, 43 mi. N of Clifton, 7 June 1935, Maguire 11886 (ARIZ, GH, NY, UC). Navajo Co., head of Little Colorado, 10 July 1912, Goodding 1147 (ARIZ, NY, RM, US). Yavapai Co., S of Prescott, 2 June 1944, Clark 11770 (GH, US). **Colorado:** Archuleta Co., Piedra, near Piedra River, 18 June 1924, Schmoll 1122 (RM). Chaffee Co., Poncha Springs, at intersection of railroad and highway along creek bed, 27 May 1968, Turner 5777 (TEX). Clear Creek Co., Brookvale, Bear Creek, Churchill 1918 (GH, MO). Conejos Co., SW of La Jara Reservoir, 19 Aug. 1986, O'Kane & Anderson 2618 (RM). Costilla Co., 61 mi. E of Montevista, La Veta Pass, 30 May 1934, Frederick & Stone 608 (NY). Custer Co., W of Westcliffe, trail to Lakes of the Clouds, 29 July 1950, Weber 5894 (COLO). Delta Co., Mule Park, 12 July 1962, Gierisch 2552 (RM). Dolores Co., Lone Cone, along water courses, Brewster s.n. (COLO). Eagle Co., McCoy, edge of meadow, 30 July 1898, Shear 5310 (RM). Garfield Co., Glenwood 1910 (GH). Gunnison Co., Sapinero, 19 June 1901, Baker 173 (MO, RM, ND, NY, POM, UC). La Plata Co., 10 mi. W of Durango, 20 June 1965, Strother 389 (TEX). Las Animas Co., Wilkins Creek, ca. 0.25 mi. NW of Stonewall Gap, 15 Aug. 1987, Neely 4635 (RM). Mesa Co., Uncompahgre Plateau, head of Escalante Canyon, 19 July 1982, Siplivinsky & Beck 4251 (COLO, RM). Mineral Co., Wolf Creek Pass, U.S. Hwy. 160, 3 mi. below summit on E side, 27 Aug. 1964, Turner 5099 (TEX). Montezuma Co., along Dolores Riv-



er, Escalante Sector, *Bye et al.* 1978 (COLO). Montrose Co., 30 mi. SW of Montrose, 28 Aug. 1937, *Rollins* 1978 (CAS, GH, MO, ND, NY, RM, US). Ouray Co., *Clements* 1907 (NY). Rio Blanco Co., 2 mi. E of Meeker, 18 Aug. 1935, *Maguire & Piranian* 12844 (MO). Park Co., Jefferson South Park, 9 Sep. 1942, *Ewan* 14706 (COLO). Rio Grande Co., along South Fork of Rio Grande River, 27 Aug. 1964, *Turner* 5095 (TEX). Saguache Co., Marshall Pass, 21 July 1960, *Barrell* 127-60 (US). **Idaho:** Bannock Co., E of Lava Hot Springs, *Everson* 1946 (NY). Bear Lake Co., 1.3 mi. N of St. Charles, 25 June 1967, *Faircloth* 4548 (NCU). Bingham Co., Ft. Hall, *Everson* 1942 (TEX). Caribou Co., 8 Mile Canyon, 12 mi. S of Soda Springs, 28 June 1960, *Cottam et al.* 16280 (UT). Cassia Co., 20 mi. S of Oakley, along Goose Creek, 2 July 1950, *J. H. & C. B. Christ* 19580 (WS). Clark Co., Kaufman, near Birch Creek, 19 July 1934, *Christ* 5818 (NY). Elmore Co., Moore's Creek, Boise River tributary, *Grandjean* 155 (RM). Franklin Co., 11 mi. NE of Preston, 5 mi. up Millcreek Canyon, 14 May 1966, *G. & G. Davidse* 391 (UC, US, WTU). Lemhi Co., 20 mi. E of Gilmore, along Birch Creek, 25 June 1947, *Hitchcock* 15766 (CAS, COLO, MO, NY, PH, POM, RM, UC, WS, WTU). Oneida Co., divide between Marsh and Malad Valleys, *Coulter s.n.* (PH). Owyhee Co., ca. 39 mi. S of Bruneau, 30 May 1968, *Turner* 5798 (NY, RM, TEX). Twin Falls Co., Twin Falls, 26 May 1912, *Bennett* 88 (RM). **Montana:** Beaverhead Co., Armstead, 20 June 1920, *E. B. & L. B. Payson* 1734 (CAS, GH, MO, RM). Broadwater Co., 4 mi. SE of Townsend, 10 June 1960, *Schmautz* JES-345 (CAS, RM, WS). Deerlodge Co., Fishtrap, ca. 25 mi. S of Anaconda, 20 June 1944, *Hitchcock & Muhlick* 9173 (CAS, GH, MO, NY, RM, UC, WS, WTU). Gallatin Co., Belgrade, low ground, 2 June 1906, *Blankenship* 681 (F, MO, POM, RM, UC, US). Jefferson Co., Boulder, 24 Apr. 1939, *Rose* 709 (RM). Madison Co., Virginia City, *Swingle* 1933 (RM, WTU). Powell Co., vicinity of Deer Lodge, *Fitch s.n.* (RM). Silver Bow Co., Lower Moose Creek, ca. 1 mi. N of Moose Creek Parking Area, 28 June 1979, *Lowry* 2270 (RM). **Nevada:** Elko Co., 3 mi. N of Ruby Valley on E side of Ruby Mts., 29 May 1968, *Turner* 5795 (TEX). Eureka Co., Eureka, 2 July 1904, *Kennedy* 838 (ARIZ, MO, RM, UC). Humboldt Co., Santa Rosa Range, NE of Winnemucca, 29 June 1967, *Gentry & Davidse* 1674 (ARIZ, COLO, GH, MO, NY, OSC, POM, UC, WTU). Lander Co., Reese River Valley, U.S. Hwy. 50, along edge of Reese River, 13 June 1964, *Spellenberg* 370 (F, NY). Lincoln Co., Geyser Ranch, 28 May 1945, *Ripley & Barneby* 6436 (NY). Nye Co., Darrough Hot Springs, Smoky Valley, 11 May 1939, *Train* 2743 (MO, NY, POM, TEX, UC, WTU). White Pine Co., canyon E of Mt. Grafton, 11 Aug. 1969, *Holmgren & Bethers* 3861 (NY, POM, US, WTU). **New Mexico:** Bernalillo Co., 8.5 mi. from San Antonito, 0.7 mi. N of Capulin Spring, 21 May 1967, *Turner* 5649 (CAS, NY, TEX). Catron Co., Mogollon Mt., near West Fork of the Gila River, 23 Aug. 1903, *Metcalf* 593 (MO, ND, NY, RM, US). Colfax Co., 1 mi. NW of Ute Gulch Camp, 17 June 1968, *Hartman* 1973 (RM, TEX). Grant Co., Pinos Altos, 2.6 mi. by road to Signal Peak E of New Mexico Hwy. 15, 25 May 1985, *Worthington* 13180 (NY, RM). Lincoln Co., Sierra Blanca, valley of Carrizo Creek, 11 June 1932, *Wilkins* 2402 (PH, US); McKinley Co., Long Canyon, 6 mi. S of Crownpoint, *Jump* 1974 (ARIZ). Mora Co., 1 mi. E of La Cueva, *Stiteler* 1949 (PH). Otero Co., near summit of pass between Hollywood and

Mescalero, 26 May 1934, *Ferguson & Ottley* 5223 (UC). Rio Arriba Co., Ortega Mts., ca. 2 mi. W of Hopewell Lake, 17 Aug. 1984, *Hill* 15167 (NY). San Miguel Co., 8 mi. E of Glorietta, along the Pecos River, 9 June 1897, *A. A. & E. G. Heller* 3681 (MO, NY, US). Sandoval Co., 24 mi. N of Jemez Pueblo, 6 June 1974, *Atwood* 6249 (NY). Santa Fe Co., near Santa Fe Recreation Area, just off New Mexico Route 475, 16 June 1964, *Perdue* 6047 (US). Taos Co., Penasco, Santa Barbara Canyon, 7 July 1936, *Marcelline* 1989 (F). **Oregon:** Crook Co., 5 mi. W of Prineville, 15 June 1928, *Pech* 15964 (OSC, PH). Grant Co., 3 mi. E of Canyon City, 5 June 1953, *Cronquist* 7087 (GH, NY, WS, WTU). Harney Co., 23 mi. S of Frenchglen, 16 May 1959, *Cronquist* 8245 (GH, NCU, NY, POM, RM, TEX, UC, WS, WTU) [approaches variety *ovata*]. Malheur Co., 3 mi. W of McDermit, 25 June 1934, *Peck* 21734 (OSC, UC). **Utah:** Beaver Co., Wah Wah Mts., Birch Creek, 4 May 1937, *Cottam* 7109 (UT). Box Elder Co., Brigham City, 9 May 1910, *Smith* 2120 (GH, NY). Cache Co., 0.25 mi. E of Wellsville, 30 May 1940, *Maguire* 18600 (NY, WTU). Daggett Co., vicinity of Flaming Gorge, 29 May 1932, *Williams* 432 (GH, MO, NY, RM). Duchesne Co., 5 mi. N of Duchesne, 6 June 1979, *Neese & Welsh* 7503 (NY). Garfield Co., 7 mi. SE of Boulder, Deer Creek, 4 May 1977, *Foster* 3661 (NY, UT). Grand Co., 2 mi. N of Warner Ranger Station, La Sal Mts., 8 July 1933, *Maguire* 313 (UC, WTU). Iron Co., ca. 15 mi. E of Cedar City, just W of the entrance to Dixie National Forest, 13 June 1969, *Meyer* 356 (UT). Millard Co., Simonsen's Ranch, along irrigation stream, 16 June 1933, *Maguire & Becraft* 3932 (GH, UC). Morgan Co., flat area below dam by old gauging station, 17 May 1987, *Peterson* 14 (NY, UT). Piute Co., 5 mi. E of Kingston on Utah Hwy. 62, 3 May 1977, *Foster* 3613 (NY, RM). Rich Co., W shore of Bear Lake, 0.7 mi. E of Pickleville, 5 July 1985, *Thorne* 3938 (GH, MO). Salt Lake Co., vicinity of Salt Lake City, *Clements* 1908 (F, GH). Sevier Co., 3 mi. S of Sevier, along stream, 8 May 1937, *Hitchcock* 2947 (GH, RM, UC, WS, WTU). San Juan Co., ca. 80 mi. S of Moab, NW flank of Abajo Mts., 12 June 1961, *Cronquist & Holmgren* 9259 (GH, NY, NCU, POM, TEX, WS, WTU). Summit Co., Goodman Ranch near Bear River, 30 June 1926, *E. B. & L. B. Payson* 4833 (MO, PH, POM, RM, UC, US); Uintah Co., E of Hayden, along Uintah River, 2 June 1933, *Graham* 8044 (F, GH, NY, US). Utah Co., near top of Price Canyon, *Malburtt* 1959 (UT). Wasatch Co., 6 mi. N of Heber City, along highway, 28 May 1968, *Turner* 5794A & 5794B (TEX). Washington Co., 5 mi. SW of Enterprise at Aspen Park Spring, 10 June 1983, *Atwood* 9366 (NY, RM). Wayne Co., Fruita, 18 May 1956, *Vickery* 587 (ARIZ, GH, POM, UT, WTU). Weber Co., Huntsville, 26 May 1940, *Brizze* 7794 (UT). **Wyoming:** Carbon Co., Baggs, 4 July 1926, *Nelson* 10720 (GH, MO, RM, UC). Park Co., *McCosh* 1878 (NY). Sweetwater Co., Uinta Mts., Henrys Fork, river bottoms, 26 June 1902, *Goodding* 1192 (CAS, F, GH, MO, NY, POM, RM, UC). Uinta Co., 1 mi. S of Lonetree, 27 July 1939, *Rollins & Munoz* 2903 (CAS, GH, US).

*Thermopsis montana* var. *montana* is widespread and highly variable but can usually be distinguished from variety *ovata* by its smaller habit, narrower leaflets and bracts, and greater tendency to spread by rhizomes. In southwestern Oregon the



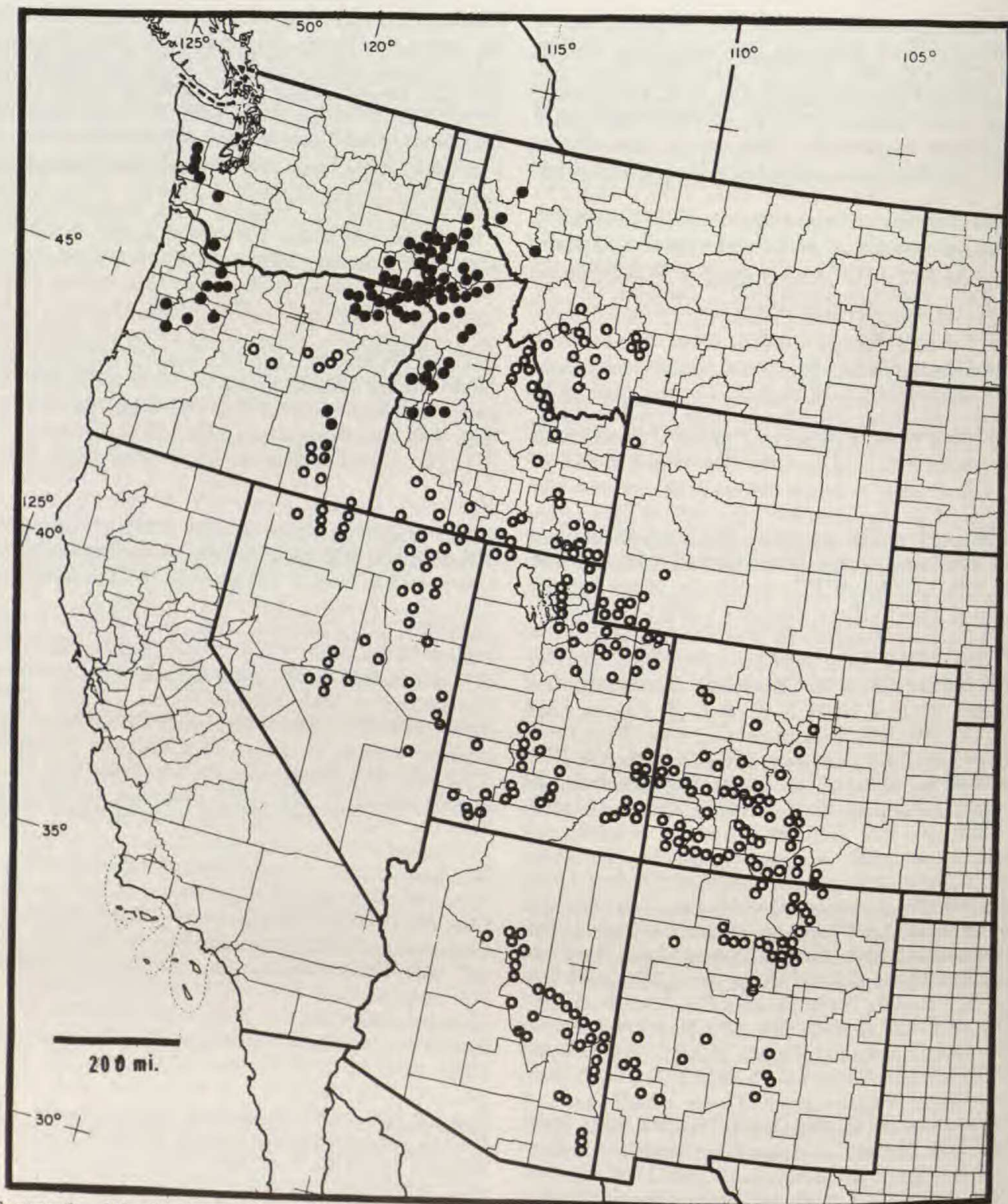


FIGURE 6. Distribution of *Thermopsis montana*: variety *montana* (open circles); variety *ovata* (closed circles).

taxa appear to intergrade. Isely (1981) recognized a "Lemhi race" (Lemhi County, Idaho) within the taxon we call *T. montana* var. *montana*. Though with somewhat broader leaflets, most of those specimens are fairly typical of *T. montana* var. *montana*.

In Arizona and most of New Mexico (from below San Juan and Rio Arriba counties) there also occurs a series of populations that are composed of rather broad-branching plants with leaves more or less like *Thermopsis montana* var. *ovata*. Unlike Isely (1981), we do not find such plants in Colorado.

The strictly erect pods distinguish *Thermopsis montana* from *T. gracilis* and from the superficially similar *T. divaricarpa*. Isely (1981) treated *T. montana* and *T. divaricarpa* as varieties of a widespread, extremely variable *T. rhombifolia*. We have found that *T. rhombifolia*, *T. divaricarpa*, and *T. montana* are clearly distinct throughout most of their ranges and do not appear to intergrade as do *T. montana* var. *montana* and *T. montana* var. *ovata*. Intermediate populations and possible hybrids are discussed under *Thermopsis divaricarpa*.



**7b. *Thermopsis montana* var. *ovata*** (Robinson ex Piper) St. John, *Torreya* 41: 112. 1941. *Thermopsis montana* subsp. *ovata* Robinson ex Piper, *Contr. U.S. Natl. Herb.* 23: 49. 1906. *Thermopsis ovata* (Robinson ex Piper) Rydberg, *Bull. Torrey Bot. Club* 40: 43. 1913. *Thermopsis rhombifolia* var. *ovata* (Robinson ex Piper) Isely, *Brittonia* 30: 470. 1978. TYPE: U.S.A. Idaho: Latah Co., "Cedar Mountain," 4 July 1893, *C. V. Piper 1489* (lectotype, selected here, WS; isoelectotypes, GH, US, WS).

*Thermopsis xylorrhiza* Nelson, (*xylorrhiza* auct.), *Bot. Gaz.* 52: 265. 1911. TYPE: U.S.A. Idaho: Canyon Co., Falk's Store, 667 m, 24 May 1910, *J. F. Macbride 99* (holotype, RM; isotypes, GH, MO, NY, RM, UC, WS).

*Thermopsis macrophylla* var. *hitchcockii* Isely, *Brittonia* 30: 469. 1978. TYPE: U.S.A. Washington: Grays Harbor Co., roadside near Humptulips, 10 July 1931, *J. W. Thompson 7342* (holotype, WTU; isotypes, GH, OSC, PH, POM, UC).

Piper's collection number 1489 was apparently a mixture of plants collected on 16 June 1893, 4 July 1893 (in fruit), and 21 June 1894 (in flower). We have selected the fruiting specimen as the lectotype. It is assumed that all of the collections came from the same site, although this is not certain because some of the labels (21 June 1894, NY) give the locality as "along streams in woods." The published type locality is given by Peck as "Cedar Mountain"; this locality was not on any of the labels numbered 1489 that we examined.

Plants 5–8(–10) dm tall, glabrate to sparsely appressed pubescent; stems erect, clustered, moderately branched, arising from a woody rootstock; branches weakly to moderately zigzagged. Leaflets broadly to narrowly elliptic or obovate, 4.5–6(–8) cm long, 1.5–3(–5) cm wide, sparsely appressed pubescent below, glabrous above, conspicuously net-veined beneath; petioles 3.2–4 cm long. Racemes 12–25 cm long; bracts narrowly elliptic. Flowers 1.9–2.2 cm long. Pods appressed pubescent.

*Distribution and ecology* (Fig. 6). Columbia and Snake River drainages of northern Idaho and adjacent states of Wyoming, Washington, and Oregon, with isolated populations along the Pacific coast of Washington and northwestern Oregon, 300–2000 m in the upper river drainages but mostly at lower elevations (10–200 m) about the mouth of the Columbia River and its immediate tributaries; flowering May–June.

*Representative specimens examined.* U.S.A. **Idaho:** Ada Co., 13 mi. E of Boise, Moore's Creek Canyon, 14 June 1947, *J. H. & C. B. Christ 16858* (NY). Adams Co., *Davis 1939* (WS); Hornet, 13 May 1915, *Mangun 139* (RM). Boise Co., 15 mi. W of Lowman, above Payette River, on road between Banks and Lowman, 31 May 1944, *Hitchcock & Muhlick 8563* (NY, WS, WTU). Butte Co., *Christ 3386* (NY). Canyon Co., Falk's Store, 10 May 1911, *Macbride 800* (F, GH, MO, NY, POM, RM, UC, US, WS, WTU). Clearwater Co., Clearwater Forest, Lolo Creek, 16 Oct. 1934, *Christ 6322* (NY); 5 mi. W of Orofino, S side of the Clearwater River, 5 May 1951, *Roeder 241* (WS). Idaho Co., 0.5 mi. from Pilot Rock, *Elwood 51* (CAS, NY, POM, UC, WS, WTU); 7 mi. SE of Elk City, 14 June 1950, *Jones 14* (CAS, GH, POM, WS, WTU); 2 mi. S of Grangeville, 29 May 1944, *Hitchcock & Muhlick 8455* (CAS, NY, RM, UC, WS, WTU). Latah Co., wooded hills just W of Troy, 24 May 1964, *Hitchcock 23465* (CAS, NY, UC, WS, WTU). Lewis Co., Mission Creek, 30 May 1924, *John et al. 6334* (UC, WS, WTU). Nez Perce Co., Aug. 1898, *Brown 6* (CAS, MO, ND, NY, PH, UC, US); 3 mi. below Lowell, 30 May 1936, *Constance & Rollins 1621* (F, GH, NCU, MO, NY, RM, UC, PH, WS, WTU); near Lewiston, 7 May 1896, *A. A. & E. G. Heller 3035* (CAS, F, MO, ND, NY, PH, UC, WTU); valley of Hatwai Creek, 28 Apr. 1892, *Sandberg et al. 68* (ARIZ, F, GH, MO, NY, POM, US). Shoshone Co., 8 mi. N of Calder, along St. Joe River, 19 May 1940, *Christ 10969* (NY); Clearwater Camp on the Little North Fork of the Clearwater River, 4 Aug. 1941, *Wilson 467* (WS). Valley Co., 5 mi. W of McCall, 24 June 1946, *Hitchcock & Muhlick 13937* (CAS, MO, NY, POM, RM, UC, WS); 9 mi. E of McCall, 11 July 1953, *Holmgren & Tillett 9542* (GH, NY, OSC, UC, WTU). Washington Co., S of Council, wet meadows along highway, 11 May 1939, *Cronquist 1151* (NY). **Montana:** Sanders Co., Dixon, 31 May 1937, *Brome 28* (MO, PH, RM, WTU); 2 mi. W of Dixon, Wolf Point, 13 May 1936, *Hitchcock 2877* (MO, ND, OSC, RM, WS, WTU). **Oregon:** Clackamas Co., Eagle Creek, high hills, 24 May 1884, *Henderson 179* (OSC, PH, WS); near base of Table Rock, *Leach 1927* (WTU). Linn Co., Monument Peak, *Gilkey 1947* (OSC, POM). Marion Co., Silverton, Spring 1871, *Hall 83* (F, POM); 6 mi. E of Brownsville, Cascade Mts., 18 June 1918, *Lawrence 1751* (OSC, US); Silver Creek Falls, 19 June 1918, *Nelson 2257* (GH). Polk Co., 2 mi. W of Grand Ronde, *Brehm 1967* (TEX). Umatilla Co., 1 mi. SE of Meacham, 23 June 1946, *Hitchcock & Muhlick 13841* (CAS, GH, MO, NY, OSC, UC, WS, WTU); between Pendleton and LaGrande, near summit of Blue Mts., 14 June 1928, *Thompson 4723* (CAS, GH, MO, US, WTU). Union Co., Kamela, 1 June 1910, *Heller 10145* (CAS, GH, PH, UC); 2 mi. S of Elgin, 20 May 1975, *Watkins & Dunn 95* (MO, NY). Wallowa Co., along summit of road between Elgin and Langdon Lake, 28 July 1950, *Kruckeberg 2487* (CAS, COLO, GH, NY, RM, UC); Walupi Canyon, 18 Aug. 1897, *Sheldon 8724* (NY, US). **Washington:** Asotin Co., Snake River, just below the mouth of the Grande Ronde, 17 Apr. 1949, *Cronquist 5701* (GH, NY, POM, UC, US, WS, WTU); SW of Anatone, along Grande Ronde River, just above Rattlesnake Creek, 22 Apr. 1949, *Cronquist 5709* (GH, NY, POM, UC, US, WTU). Columbia Co., Dayton, between hospital and Touchet River, 3 May 1983, *Baird 51* (NY); Blue Mts., 4 mi. N of Table Rock, 20 July 1935, *Constance et al. 1278* (MO, WS). Grays Harbor



Co., N of Aberdeen and Hoquiam along U.S. Hwy. 101, 31 May 1987, *Boufford & E. W. Wood* 23757 (A, CAS, MO, NCU, NY); ca. 20 mi. N of Hoquiam, 24 June, *Hitchcock* 19872 (COLO, OSC, POM, UC, WTU); between New London and Humptulips, 28 June 1933, *Jones* 3937 (CAS, POM, RM, UC, WTU); open burns near Humptulips, 30 May 1940, *Thompson* 14606 (CAS, GH, MO, NY, PH, POM, RM, UC, US). Lewis Co., Chenalis, Oxford Prairie, 12 June 1897, *Lamb* 1197 (CAS, F, MO, NY, PH, UC, WS). Walla Walla Co., 2 mi. S of Walla Walla, 24 May 1944, *Hitchcock & Muhlick* 8274 (CAS, NY, RM, UC, WS, WTU); 1 mi. NE of Walla Walla, flats near Mill Creek, 2 May 1936, *Moore* 23 (UC, WS). Whitman Co., 1 mi. N of Colfax, 18 May 1935, *Hitchcock & Samuel* 2594 (OSC, RM); Kamiack, 15 June 1893, *Moore* 1489 (US, WTU); Dusty, 3 mi. W of Colfax, 14 May 1922, *Parker* 355 (NY, OSC, POM, WS).

This variety differs from *Thermopsis montana* var. *montana* in its relatively robust habit, moderately branched stems, and broader leaflets and bracts.

Plants similar to *Thermopsis montana* var. *ovata* also occur as populational variants in Arizona, most of New Mexico, parts of southern Utah, and occasionally in Colorado, as discussed under *T. montana* var. *montana*. Our treatment is like that of Isely (1981), who positioned variety *ovata* within his broad *T. rhombifolia*, except that we would include his *T. macrophylla* var. *hitchcockii* within *T. montana* var. *ovata*. We do not believe that the Pacific coast plants (= *T. macrophylla* var. *hitchcockii*, sensu Isely) differ appreciably from plants of the interior montane regions that Isely places within *T. rhombifolia*. The disjunct distribution of the Pacific coastal populations is thought to represent founder populations, perhaps dispersed by periodic flooding events and subsequent establishment of propagules from populations along the upper Columbia and Snake River drainages. One may assume that these northern Pacific coast populations are more closely related to the southern populations of *T. californica*, as suggested by Isely's treatment. Although both taxa have upright pods, the distribution of *T. californica* is interrupted in Oregon by the quite distinctive *T. gracilis*, which has divergent pods. All of the specimens of *T. montana* var. *ovata* that we have examined (including the Pacific coastal populations) have strictly erect pods, yet have other characters of the Rocky Mountain species, namely *T. montana* var. *montana*. If one accepts the taxonomic concepts espoused by Isely (1981) in which *T. divaricarpa* and *T. montana* are reduced to varietal entities of a widespread, highly variable *T. rhombifolia*, one is compelled by morphological considerations to include both *T. gracilis* and *T. cali-*

*ifornica* also as part of the *T. rhombifolia* complex, the morphological boundaries between *T. montana* var. *ovata* and *T. californica* being at least as weak as those between *T. rhombifolia* and *T. divaricarpa* or *T. montana*.

**8. *Thermopsis rhombifolia*** (Nutt. ex Pursh) Richardson, Bot. App. 737. 1823. *Thermia rhombifolia* (Pursh) Nutt., Gen. N. Amer. Pl. 1: 282. 1818. *Scolobus rhombifolius* (Nutt. ex Pursh) Raf., Amer. Monthly Mag. Crit. Rev. 4: 193. 1819. *Drepilia rhombifolia* (Nutt. ex Pursh) Raf., N. Fl. 2: 53. 1837. TYPE: U.S.A. North Dakota: Mercer Co., near Fort Mandon, *Bradbury* 1810 (lectotype, selected here, PH, A. B. Lambert herbarium).

*Thermopsis arenosa* Nelson, Bot. Gaz. 25: 276. 1898. *Thermopsis rhombifolia* var. *arenosa* (Nelson) Larisey, Ann. Missouri Bot. Gard. 27: 251. 1940. TYPE: U.S.A. Wyoming: Albany Co., Laramie Hills, 16 June 1897, *A. Nelson* 3182 (holotype, RM; isotypes, ND, RM, [2 sheets] UC, US).

*Thermopsis annulocarpa* Nelson, Bull. Torrey Bot. Club 26: 239. 1899. *Thermopsis rhombifolia* var. *annulocarpa* (Nelson) L. Williams, Ann. Missouri Bot. Gard. 23: 450. 1936. TYPE: U.S.A. Wyoming: Carbon Co., Ferris Mountains, vicinity of Fort Steele, "among the rocks on the naked slopes near their summits," 25 July 1898, *Elias Nelson* 4971 (holotype, RM; isotype, NY).

Larisey (1940) designated a Nuttall collection (PH) as the type of *Thermopsis rhombifolia*; however, Pursh cited only a *Bradbury* collection, listing *Cytisus rhombifolius* Nutt. as a nomen nudum from Fraser's *Catalogue* without citing a Nuttall collection.

Plants dwarf but robust, 1.2–3 dm tall, glabrate to appressed pubescent; stems slender, erect, or ascending, solitary or clustered, few-branched, arising from a woody rootstock or rhizomes; branches ascending at 25–50°, weakly zigzagged. Leaflets elliptic to obovate or narrowly elliptic, 1.7–3.3 cm long, 0.6–2 cm wide, acute to obtuse, sometimes short mucronate, appressed pubescent to sparsely tomentose or glabrate below, glabrous above, lateral veins 5–7 pairs, conspicuously net-veined beneath; petioles 0.8–2.2 cm long; stipules persistent, ovate to very widely ovate or elliptic to widely elliptic, 1–2.6 cm long, 0.5–1.5(–2.2) cm wide, cuneate to oblique, acute to obtuse and short mucronate. Racemes 4–12 cm long, with 5–15 flowers, in whorls of 2–3 or scattered; peduncles 1–4 cm long; pedicels 3–7 mm long, glabrate to densely appressed pubescent; bracts deciduous, el-



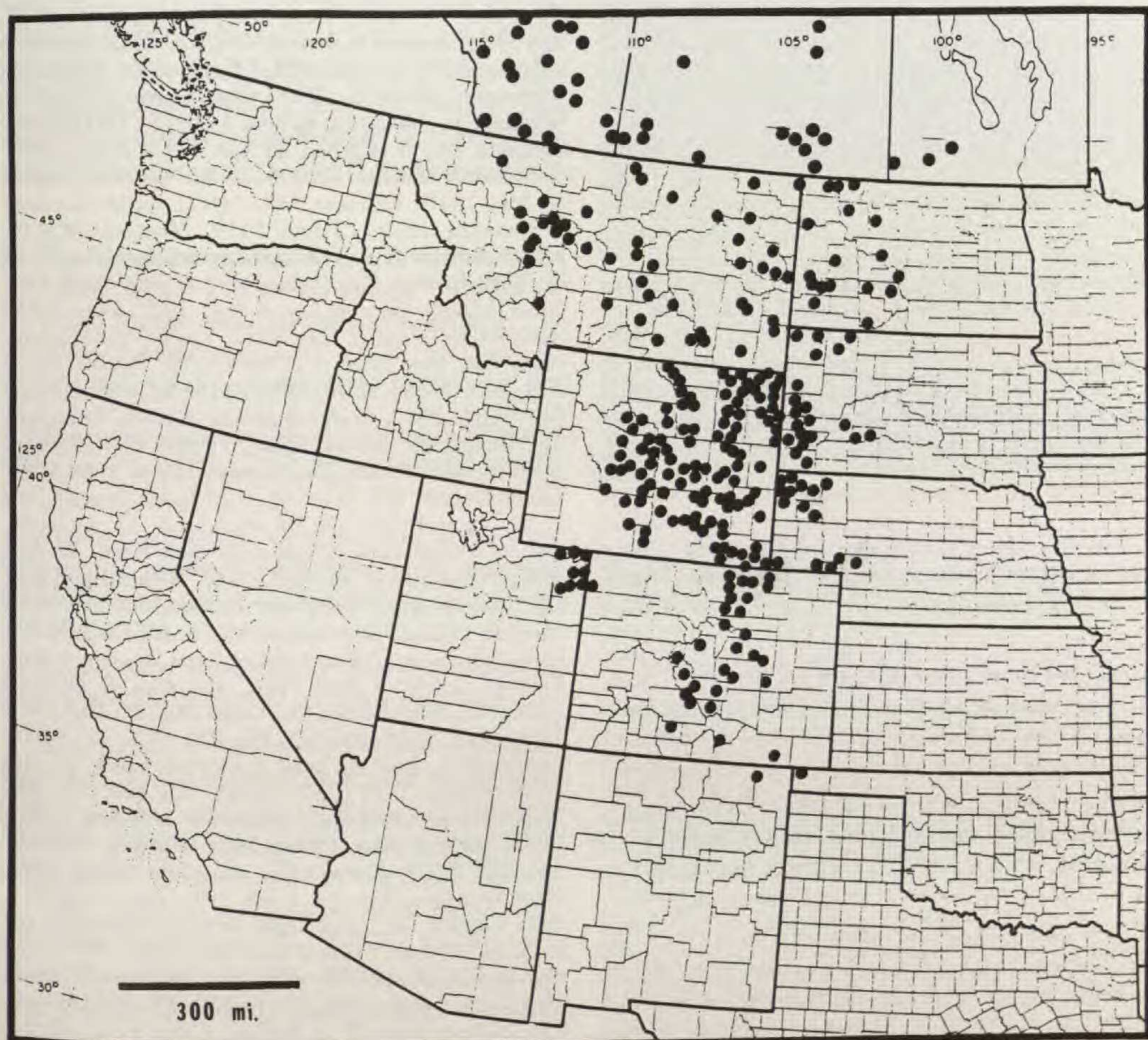


FIGURE 7. Distribution of *Thermopsis rhombifolia*.

lipoitic to obovate, 5–9 mm long, 3–5 mm wide. Flowers 1.9–2.1 cm long; calyx (6–)8–10(–12) mm long, 4.5–6 mm wide at the limb, lobes (3–)4–5 mm long, as long as or shorter than tube; wings asymmetrically oblong–very widely ovate; keel asymmetrically oblong–widely elliptic; ovary glabrate to appressed puberulent; ovules 12–14. Pods arcuate to annular, divergent, 3–7 cm long, 0.4–0.7 cm wide, glabrate to sparsely tomentose. Seeds 2–10, brown, elliptic with a rostrum, 3.5–4 mm long, 2.5 mm wide. Chromosome numbers  $2n = 18$ .

*Distribution and ecology* (Fig. 7). Central Great Plains of Canada and the United States from central Alberta and Saskatchewan to northeasternmost New Mexico, largely confined to relatively xeric grasslands in deep alluvial soils but extending into the lower canyons of the front range of the Rocky Mountains, 1000–2000 m, to 3000 m along roadsides; flowering May–June.

*Representative specimens examined.* CANADA. **Alberta:** ca. 26 km NE of Edmonton, 1 km SW of Fort Saskatchewan, 20 June 1959, *Sheller & Stone 3034* (US); 20 km W of Cochrane, 1 July 1979, *Watton 24* (COLO, MO, NY, OSC, PH). **Manitoba:** on side of Manitoba Hwy. 1 in the sand hills, 9 June 1950, *Dore 10658* (GH, NY). **Saskatchewan:** Cypress Hills Provincial Park, 1 July 1947, *Breitung 4200* (MO, RM). U.S.A. **Colorado:** Arapahoe Co., near Denver, 13 May 1917, *Clokey 2793* (ARIZ, F, GH, RM, TEX, UC, US). Boulder Co., 10 mi. NE of Boulder, White Rocks, on Gunbarrel Hill, 18 May 1967, *Turner 5634* (RM, TEX). Chaffee Co., 5 mi. SW of Buena Vista, 13 June 1967, *Johnson 80* (MONTU, NCU, TEX). Douglas Co., 2 mi. W of Franktown, 27 June 1937, *Beetle 1477* (CAS, NY, WTU). Elbert Co., 2 mi. N of Simla, 23 June 1937, *Ownbey 1296* (COLO, GH, MO, MONTU, NY, RM, UC, WS). El Paso Co., near Ramah, 25 May 1947, *Moldenke 19401* (PH, RM). Jefferson Co., E of Golden, 8 May 1941, *Ehlers 8064* (COLO, TEX). Lake Co., Tennessee Fork, 16 June 1933, *Applegate 8524* (F). Larimer Co., 7 mi. S of Fort Collins, 3 May 1965, *Irving 6511* (TEX). Las Animas Co., N of Mesa de Maya, 28 Apr. 1948, *Rogers 5664* (COLO, TEX). Lincoln Co., 2.5 mi. E of



- Lincoln, 7 May 1987, *Falb & Miercort 23A* (RM). Moffat Co., Blue Mountain, 8.2 mi. N of U.S. Hwy. 40, 6.5 airline mi. NNE of Dinosaur, 11 June 1971, *Holmgren et al. 5162* (CAS, NY, US, WTU). Park Co., Como, 15 June 1892, *Hughes 42* (GH). Saguache Co., 2 mi. S of Villa Grove on U.S. Hwy. 285, 27 May 1968, *Turner 5774* (TEX). Weld Co., Pawnee Buttes, 1 July 1906, *Dodds 2111* (COLO). **Montana:** Big Horn Co., road to visitor center at Yellowtail Dam, 16 May 1983, *Lichvar 5666* (RM). Blaine Co., Chinook, 26 May 1937, *Wellington 1049* (MONTU). Carter Co., Medicine Rocks State Park, 28 Apr. 1986, *Mooers et al. 1085* (MONTU). Cascade Co., ca. 14 mi. W of Great Falls, 11 May 1956, *Booth 56224* (GH, MONTU). Chouteau Co., Fort Benton, June 1883, *Anderson 547* (US). Custer Co., 5 *Woolfolk* 1936 (GH, PH, POM, RM). Daniels Co., *Von Kuster 12* (RM). Dawson Co., 5 mi. SW of Glendive, 20 May 1965, *McMullin 308* (UC). Fergus Co., 3 mi. up Fords Creek turn off, 19 May 1988, *Lipscomb 1* (MONTU). Gallatin Co., bench gravel, 6 July 1910, *Spragg 245* (MONTU). Garfield Co., 15 mi. N of Jordan, 13 May 1968, *Woodland 1632* (CAS). Glacier Co., S of Hudson Bay Divide, 31 May 1958, *Harvey 66750* (MONTU). Judith Basin Co., Long's Ranch, 8 June 1900, *Wilcox 388* (US). Lewis and Clark Co., ca. 4 mi. W of Wolf Creek, 2 July 1948, *Hitchcock 17984* (CAS, COLO, GH, MONTU, NY, POM, UC, WS). McCone Co., Wolf Point, 19 May 1937, *Buck-of 546* (MONTU, WTU). Musselshell Co., Roundup, 11 May 1937, *Syblon 522* (CAS, RM, UC, WTU). Petroleum Co., Flatwillow, 28 May 1936, *Wickland 18* (MONTU). Powder River Co., 18 May 1975, *Lackschewitz 5937* (MONTU). Prairie Co., 10 mi. S of Brockway, 5 May 1941, *Koch 4* (MONTU). Rosebud Co., along U.S. Hwy. 212, ca. 10–15 mi. W of Ashland, 18 July 1967, *Hess 762* (MO). Sheridan Co., Westby, 17 July 1927, *Larsen 20* (GH, MO, PH, RM). Sweet Grass Co., Big Coulee Creek, *Blankinship 1902* (MONTU, WS, WTU). Teton Co., 22 mi. SW of Chouteau, *Finley 1963* (MONTU); Collins, *Jones 1904* (UC). Toole Co., Sweetgrass, *Recup 1918* (NY). Valley Co., Fork Peck, 26 May 1919, *Ramsden & Lackschewitz 345* (MONTU). Wibaux Co., Hodges, *Griffins 1936* (MONTU, RM, TEX, WTU). Yellowstone Co., 10 mi. NW of Billings on Lavina Road, 3 June 1973, *Doles 563* (UT). **Nebraska:** Box Butte Co., Hemingford, 1 June 1950, *Kiener 24623* (US). Cheyenne Co., 2 mi. W of Sunol, 18 May 1970, *Stephens 38111* (NCU). Deuel Co., Rush Creek, *Rydberg 1891* (GH, US). Keith Co., E of Cedar Point Biological Station, 7 June 1983, *Sutherland 5598* (NY). Kimball Co., 8 mi. SW and 1.5 mi. S of Bushnell, 18 May 1970, *Stephens 38143* (GH, NY). Garden Co., Ash Hollow State Park, W of Lewellen on U.S. Hwy. 26, 19 May 1976, *Churchill 7323* (MO, NY). Sheridan Co., 13 mi. N of Hay Springs, 5 May 1964, *Nixon 6* (RM). Sioux Co., 7.5 mi. S of the junction of Nebraska Hwys. 2 & 71 on Hwy. 71, 27 May 1972, *Churchill 77* (MO, NY). **New Mexico:** Union Co., Capulin Mountain National Monument, 17 July 1941, *A. & R. A. Nelson 4650* (MONTU). **North Dakota:** Billings Co., Cedar Canyon, 9 June 1952, *Clausen 8194* (GH). Burleigh Co., Bismarck, *Lantermann 1891* (MO, NY, WTU). Burke Co., Portal, 18 June 1903, *Barber 360* (GH). Divide Co., 25 May 1961, *Stevens 2377* (UC, US). Dunn Co., Killdeer Historical Site, *Stevens 1951* (US). Grant Co., Pretty Rock National Wildlife Refuge, 23 Aug. 1907, *Bell 1197* (UC). Mercer Co., Missouri River Valley, 8 mi. N of Knife River, 29 June 1941, *Stevens 905* (NCU, UC, US). Morton Co., Glen Ullin, May 1891, *Holzinger 5* (GH). Mountrail Co., 12 July 1960, *Stevens & Moir 2289* (NCU, UC). Slope Co., *Atkinson 1935* (F, NCU, RM, UC). Stark Co., Dickinson, *Whitman 1949* (US). Ward Co., *Haigh 1900* (NY). Williams Co., Williston, *Stevens 1918* (F). **Oklahoma:** Cimarron Co., N of Mesa, 28 Apr. 1948, *Rogers 5664* (US). **South Dakota:** Butte Co., 5 mi. N of Belle Fourche, 23 May 1970, *Stephens 38357* (NY). Custer Co., head of Blocktail Gulch, 12 Apr. 1910, *Murdoch 4020* (F, NY). Fall River Co., Ochich, 8 Apr. 1911, *Nelson 2724* (F, RM). Jackson Co., Cedar Pass, 17 July 1913, *Over 6113* (COLO). Harding Co., 4 Aug. 1927, *Over 17438* (US); Rabbit Butte, 1 May 1912, *Vesher 553* (F). Lawrence Co., near Lead, 17 June 1929, *Palmer 37352* (GH, MO, NY, US). Meade Co., 40 mi. NW of Rapid City, 9 July 1947, *Crider & Atkins 44* (RM). Pennington Co., Black Hills, Harney Peak, 8 July 1927, *Hayward 1961* (F, RM). Perkins Co., Lemmon, *Halse 1969* (OSC). **Utah:** Daggett Co., 6 air mi. N of Dutch John, 7 June 1979, *Atwood 7284* (NCU). Uintah Co., ca. 14 air mi. NW of Vernal along Tridell–Dry Fork Road, 31 June 1983, *Neese 14116* (MONTU, NY). **Wyoming:** Albany Co., Laramie Mts., Telephone Canyon, 30 May 1936, *Ownbey 1027* (COLO, MO, MONTU, RM, WS, WTU). Campbell Co., ca. 8 air mi. SE of Reno Junction at Little Thunder Creek, 3 June 1978, *Hartman & Dueholm 5896* (NY, RM). Carbon Co., Como Bluff, 25 May 1947, *Porter 4162* (CAS, MO, NY, PH, RM, TEX, UC, WTU). Converse Co., near the head of La Prele Creek, 27 June 1950, *Porter 5374* (CAS, COLO, GH, MO, NY, RM, TEX, WTU). Crook Co., 8 mi. NW of Hulett, 6 June 1935, *Ownbey 646* (COLO, MO, MONTU, NY, RM, UC, WS, WTU). Fremont Co., ca. 20 mi. SW of Lander along Wyoming Hwy. 28, 2 July 1983, *Evert 5282* (NY, RM). Goshen Co., sandy hills between Wheatland and Veteran, 19 June 1953, *Porter 6235* (RM, WTU). Hot Springs Co., 20 mi. NW of Thermopolis along Wyoming Hwy. 120, 3 July 1983, *Evert 5312* (NY, RM). Johnson Co., Bighorn Mts. W of Buffalo, Circle Park, 23 July 1958, *C. L. & M. W. Porter 7562* (CAS, RM, UC, WTU). Laramie Co., Pine Bluffs, 2.5 mi. S of U.S. Hwy. 30 and Interstate Hwy. 80, 6 June 1969 *Cox & Dunn 1091* (MO). Natrona Co., 5 mi. W of Powder River, 5 July 1979, *Dueholm 7760* (NY, RM). Niobrara Co., 22.5 air mi. NW of Lusk and 14.5 air mi. SW of Lance Creek, 2 June 1978, *Nelson 1591* (RM). Platte Co., 21.5 air mi. N of Guernsey, 31 May 1978, *Nelson 1540* (NY, RM, UC). Sheridan Co., 9 mi. S of Sheridan, 30 June 1979, *Dueholm 7542* (NY, RM). Sweetwater Co., 16 mi. W of Wyoming Hwy. Rt. 789, 15 July 1973, *Hill 985* (RM). Washakie Co., S of Ten Sleep, 25 July 1901, *Goodding 353* (F, GH, MO, NY, RM, US). Weston Co., 3.5 air mi. NW of Osage, 22 May 1984, *Marriott 6214* (NY, RM).

Larisey (1940) accepted three varieties under this species, but all of them were reduced to *Thermopsis rhombifolia* var. *rhombifolia* by Isely (1981). Although Isely's treatment extended the parameters of *Thermopsis rhombifolia* to include the long-recognized species *T. montana* and *T. divaricarpa*, which we do not accept, we agree that recognition of varieties within our narrower concept of *T. rhombifolia* is not justified. *Thermopsis rhombifolia* does not appear to intergrade with



either *T. divaricarpa* or *T. montana*, but the occasional hybrid or hybrid swarm is believed to occur between at least *T. rhombifolia* and *T. divaricarpa*, especially in Albany County, Wyoming. The name *T. arenosa* is probably based on such hybrid variants (see discussion under *T. divaricarpa*).

9. ***Thermopsis robusta*** Howell, *Erythea* 1: 109. 1893. TYPE: U.S.A. California: "California Coast Range, near the Oregon boundary," *T. Howell* 1884 (holotype, ORE; isotypes, F, GH, NY [2 sheets], US, WS, WTU).

Some of the apparent isotypes are labeled "Coast Mts., Curry Co., Oregon" (GH) and "Oregon, Coast Mountains, fortieth parallel" (F, NY, US, WTU), while another is labeled "Oregon, Coast Mountains, forty-second parallel" (WS). We have accepted the location as given in the protologue (above), which would place the actual type locality in California, probably Humboldt or Siskiyou County to judge from the specimens we have examined.

Plants robust, 8–18 dm tall, densely tomentose; stems thick, erect, clustered, well-branched, arising from a woody rootstock; branches ascending at 30–50°, strongly zigzagged. Leaflets elliptic to widely elliptic or ovate, 6.5–11 cm long, 2.5–6.5 cm wide, acute to acuminate, short mucronate, tomentose, lateral veins 9–12 pairs, not conspicuously net-veined beneath; petioles 2.2–3.5 cm long; stipules persistent, widely ovate to nearly lanceolate, 1.5–5.5 cm long, 0.7–3 cm wide, oblique to cuneate, acuminate. Racemes 20–45 cm long, with 20–40 flowers, in whorls of 2–5 or scattered; peduncles 7–10 cm long; pedicels 4–8 mm long, densely tomentose; bracts persistent, ovate, 8–14 mm long, 3–8 mm wide. Flowers 1.6–1.8 cm long; calyx 7–9 mm long, 5–8 mm wide at the limb, lobes 2–4 mm long, as long as or shorter than tube; wing and keel petals asymmetrically oblong-rhombic; ovary densely tomentose; ovules 10–13. Pods arcuate, divergent, 4.5–6.5 cm long, 0.4–0.5 cm wide, densely tomentose. Seeds 5–10, brown, reniform without a rostrum, 3.5–4 mm long, 2 mm wide.

*Distribution and ecology* (Fig. 1). Known only from northwestern California, Humboldt and Siskiyou cos., along ridgetops, 150–1500 m; flowering May–June.

*Specimens examined*. U.S.A. California: Humboldt Co., ca. 12 mi. SW of Orleans, Bee Mt., *Quick* 59-42 (CAS, COLO, TEX); 11 mi. from Orleans on Bar Shanty Road, 6 July 1956, *Tillett* 620 (POM); E of Korbelt, Bald Mt., on trail to Blohn's cabin, June 1951,

*Vollmer & Beane* 146 (CAS, POM, WTU); near Orleans, 19 May 1931, *Wieslander* 7 (RM, UC). Siskiyou Co., 11 mi. N of Somes Bar, shady forest near Camp Three, 22 June 1954, *Hitchcock* 20223 (NY, WTU); 9.5 mi. N of Klamath River, Cedar Camp Road, 11 July 1950, *Hoffman* 3643 (UC); Prospect Hill, 1220 m, 18 July 1950, *Tracy* 19220 (UC); Prospect Hill, 20 July 1950, *Tracy* 19213 (POM, UC, WTU); near State Creek, 12 June 1928, *Wieslander* 129 (JEPS). County unknown, coast of California, *Vasey* 1876 (GH).

*Thermopsis robusta* is a localized, robust endemic of northwestern California. Because of its habit, large leaflets, and densely pilosulous vestiture it is superficially similar to *T. macrophylla*. Both Larisey (1940) and Isely (1981) included *T. robusta* within their concept of *T. macrophylla* var. *macrophylla*. We believe it is more closely related to *T. gracilis*, to judge from its divergent pods and distribution.

10. ***Thermopsis villosa*** (Walter) Fernald & B. G. Schubert, *Rhodora* 50: 201. 1948. *Sophora villosa* Walter, *Fl. Carol.* 134. 1788. TYPE: U.S.A. North Carolina: without definite locality or date, *Walter s.n.* (holotype, BM not seen). Typification of this plant is thoroughly discussed by Fernald & Schubert in their transfer of the species from *Sophora* to *Thermopsis*.

*Thermopsis caroliniana* M. Curtis, *Amer. J. Sci.* 44: 80. 1843. TYPE: U.S.A. North Carolina: Haywood Co., "in sylvis montanis," *M. A. Curtis* 1839 (holotype, GH; possible isotypes, PH, NY).

Plants delicate, 6–18 dm tall, glabrate (densely villous inflorescences); stems thick, erect, solitary or clustered, few-branched, arising from a woody rootstock; branches spreading at 45–60°, moderately zigzagged. Leaflets elliptic, 4–9.5 cm long, 1.8–4.4 cm wide, acute to obtuse, glabrate above, sparsely villous below, lateral veins 6–8 pairs, conspicuously net-veined beneath; petioles 2–5(–6) cm long; stipules persistent, elliptic to ovate, 1.5–4.5 cm long, 0.9 to 2.4 cm wide, oblique to cuneate, acute to obtuse. Racemes 15–50 cm long, with 10–50 flowers, scattered or in whorls of 2–3; peduncles 6–13 cm long; pedicels 2–3 mm long, densely villous; bracts deciduous, widely ovate to widely obovate, 5–7 mm long, 5–6(–8) mm wide. Flowers 1.7–1.9 cm long; calyx 7–8 mm long, 5–6.5 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wing and keel petals asymmetrically oblong-rhombic; ovary velutinous; ovules 12–16. Pods straight to slightly arcuate, erect, 4–5.5 cm long, 0.4–0.6 cm wide, densely tomentose to villous. Seeds 7–12, olive brown, elliptic with a



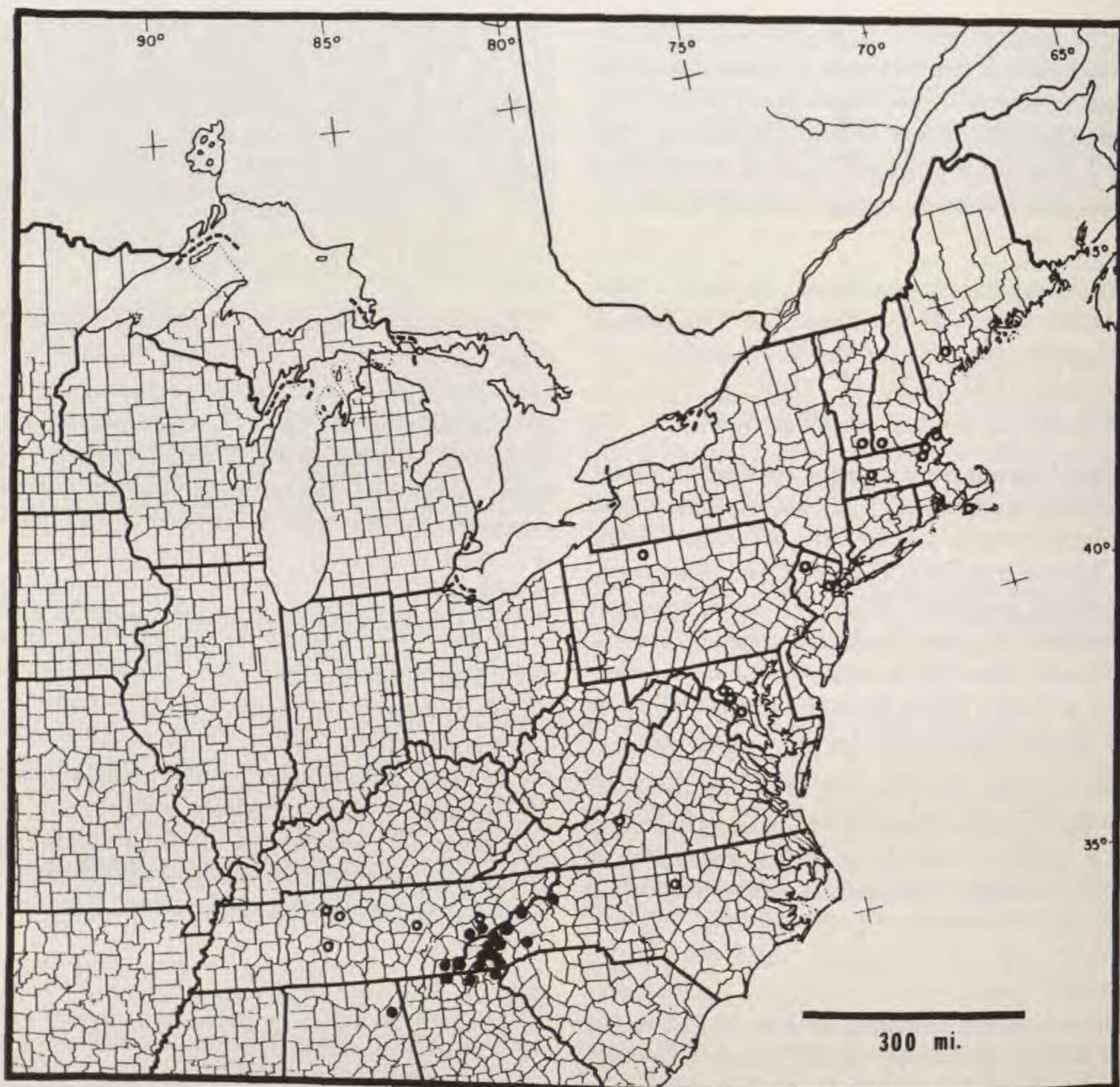


FIGURE 8. Distribution of *Thermopsis villosa*: collections thought to be native (closed circles); collections thought to be introduced or cultivated (open circles).

rostrum, 3–3.5 mm long, 1.8–2 mm wide. Chromosome number,  $2n = 18$ .

**Distribution and ecology** (Fig. 8). Native to eastern Tennessee, western North Carolina, northeastern Alabama, northern Georgia, and closely adjacent South Carolina, cultivated northward to Maine, scattered localized populations in open areas of deciduous oak woodlands, mostly 1000–1600 m; flowering May–June(–July).

**Representative specimens examined.** U.S.A. **Alabama:** DeKalb Co., 6 mi. N of Dawson, 2 July 1943, Harper 3941 (F, GH, MO). **Georgia:** Fannin Co., near Three Forks Mountain, 28 June 1983, Coile et al. 3736 (RM), 23 July 1909, Smith 2475 (F). Rabun Co., Tallulah River, Small 1893 (F, GH, MO, NY, PH, UC, US). Union Co., Brasstown Bald Mt., 15 July 1908, Howell 393 (US). **Maine:** Hancock Co., Reef Point Gardens, Spaulding 582 (GH). **Maryland:** Prince Georges Co., Hermann 18409 (RM). **Massachusetts:** Hampshire Co.,

Northampton, railroad right-of-way, Ahles 78850 (TENN). Middlesex Co., Framingham, Pike exit to Massachusetts Hwy. 9, 27 June 1975, Ahles 80370 (NEBC); Wilmington, W side of Interstate Hwy. 93, 22 June 1986, Boufford & Wood 23650 (CAS, NEBC, MO, PH). **New Hampshire:** Cheshire Co., Boufford 6134 (MO). **New Jersey:** Sussex Co., Edwards 1971 (NCU). Union Co., Moldenke et al. 30109 (ARIZ, LL). **North Carolina:** Avery Co., 0.5 mi. N of Cranberry on U.S. Hwy. 19E, 17 June 1958, Ahles & Duke 43574 (NCU). Cherokee Co., Notlely River near North Carolina Hwy. 60, 6 June 1953, Radford & Haesloop 7187a (NCU); Rugel 1842 (NY). Clay Co., base of Doe Knob, Buck Creek, 24 July 1951, Godfrey 51485 (TENN, US); NE of Chunky Gal Mt., along Buck Creek Road, 26 June 1970, Leonard et al. 3314 (NCU). Haywood Co., 1.6 mi. N of Cove Creek, 5 June 1958, Ahles & Duke 42242 (NCU). Henderson Co., ca. 1 mi. N of Lake Logan, 12 June 1964, Wilbur 7142 (GH, UC). Jackson Co., near Soco Falls, 6 July 1940, Hood 109 (MO); Soco Gap, ca. 3 mi. W of U.S. Hwy. 19, 1 July 1954, Sargent 6851 (POM, RM, WTU). Macon Co., near Highlands, Biltmore Herbarium 1332b (F, GH, MO, NCU, NY, US); 3 mi. SE of Sasfras



Gap, 18 June 1969, *Leonard & Russ 2512* (COLO, NCU, POM, TENN, UC, WTU); 6.7 mi. W of Wayah Valley Ranch, Arrowood Glade, 29 June 1970, *Turner 6072* (F, GH, NY, RM, TEX, WTU). Madison Co., *Ahles & Duke 46380* (NCU, NY). Swain Co., along stream, 12 June 1982, *Churchill 82698* (RM); 1.3 mi. from North Carolina Hwy. 28 on Mica Knob Road, 6 June 1956, *Bell 3200* (GH, NCU). Transylvania Co., U.S. Hwy. 276 near Pink Beds, 23 Sep. 1957, *Freeman 57819* (NCU); along motor road in Pink Beds, *Ripper 307* (RM). **Pennsylvania:** McKean Co., *Fogg & Wherry 9818* (PH). **Tennessee:** Blount Co., Cades Cove, near Crib Gap, *Hoss 1954* (TENN). Cumberland Co., *Adams 1962* (NCU, TENN, US). Davidson Co., NW Nashville, at intersection of Marrowbone and Eaton's Creek Roads, 17 June 1968, *Kral 31489* (NCU, TENN). Maury Co., just S of and above Rockdale on U.S. Hwy. 43, 26 June 1970, *Kral 39741* (GH, MO, NY); Harpeth hills near Nashville, *Gattinger 1879* (GH, MO, NY, US). Polk Co., ca. 1.5 km SE of summit of Big Frog Mt., 14 July 1983, *Z. E. & J. B. Murrell 389* (TENN). **Vermont:** Windham Co., *Charette 3345* (MO), and *3349* (NEBC). **Virginia:** Roanoke Co., *Uttal 6228* (NCU).

*Thermopsis villosa* is a distinctive, stiffly erect species of the southern Appalachian ridges and upper valleys. *Czefranova* (1970) treated it (as *T. caroliniana*) as the only member of series *Caroliniana*. It is superficially similar to the Californian *T. macrophylla*, as noted by Gray (1848a), in having densely villous inflorescences and closely compacted erect pods but differs markedly from that species in its much more slender, strict habit and glabrate foliage.

Sporadic, locally naturalized populations of this taxon occur from Virginia, northeastward to Maine. Fernald (1950) did not account for *T. villosa* in his treatment of *Thermopsis* for the northeastern United States, nor did he comment on the clearly naturalized populations of this species outside of its natural distribution (Fig. 8).

The species was taken into cultivation early on. Gray (1848a) stated "I raised the plant in the Cambridge Botanic Garden (where it is perfectly hardy) from seeds . . . communicated by Mr. Buckley." No doubt the species is still retained in the occasional garden or has persisted in gardens long vacated. One collection is known from Hawaii (Oahu, "Maui of Kawaiiki ditch intake," 30 Apr. 1939, *Degener 17363*, GH). We also believe that the numerous collections near Nashville, first made by Gattinger in the Harpeth hills in 1875 (MO, TENN, US), may also be locally naturalized populations.

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